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P. J. Chisholm

The Anatomy in Relation to Feeding Habits of *Perla cephalotes* Curtis (Plecoptera, Perlidae) and Other Plecoptera

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TRANSACTIONS OF THE SOCIETY FOR BRITISH ENTOMOLOGY

VOL. 15 DECEMBER 1962 PART V

The Anatomy in Relation to Feeding Habits of *Perla cephalotes* Curtis (Plecoptera, Perlidae) and Other Plecoptera

By P. J. Chisholm

(De La Salle Training College, School of Education, The University of Manchester)

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(1) Introduction

The anatomy and morphology of the head and mouthparts of various mandibulate insects are described and figured in many standard works on zoology and entomology, as well as in taxonomic papers. Nevertheless, little has been done to show how the mouthparts function in relation to the feeding habits. The main exceptions are the works of Popham (1959) on the Dermaptera and of Popham (1961) on the cockroach *Periplaneta americana* (L.).

Amongst mandibulate winged insects the most primitive orders are the Ephemeroptera and the Odonata. The Ephemeroptera are highly specialised, the adults never or seldom feeding, while the nymphs of many species are adapted to algal feeding. In the Odonata, on the other hand, the nymphs are carnivorous and the mouthparts of the adults are adapted for catching their prey and feeding on the wing. These specialisations mask, to a large extent, the primitive features of the head and mouthparts. In the stone-flies, however, the adults possess a primitive level of organisation and a number also have functional mouthparts, while the nymphs show a wide range of feeding habit from detritus to algal feeding or to carnivory.

It seems reasonable to expect that a study of the functional morphology of the head and neck of the Plecoptera would give a valuable insight into the organisation of the head and mouthparts of the early Pterygota and also possibly throw some light on the phylogenetic affinities of the order.

Of the more notable publications on plecopteran anatomy and morphology are Schoenemund's (1912) paper, which gives a short, descriptive account of the morphology and biology of the grown nymphs of the German species of *Perla,* and Schwermer's (1914) work on the biology and anatomy of *Perla marginata* Stephens which is a similar descriptive account of the biology and anatomy. Imhof's (1881) study of the anatomy of *Perla maxima* (=*marginata* Stephens) gives a more detailed account of the general anatomy of this species, particularly of the nervous system, as does also Wu's (1923) paper on the morphology, anatomy and ethology of an un-named species of *Nemoura.*

A number of taxonomic papers have been published on stone flies, the most notable of which are Classen's (1931), on plecopteran nymphs of America, and Per Brinck's (1949) paper on Swedish stone flies.

These papers on plecopteran anatomy, morphology and taxonomy are of a general descriptive nature and either omit or briefly refer to the functional morphology of these insects.

As yet no comparative account of the nymph and adult of any species of stone-fly has been published, though this is a matter worthy of study since the nymphs and adults of some species of the Systellognatha display profound differences in structure.

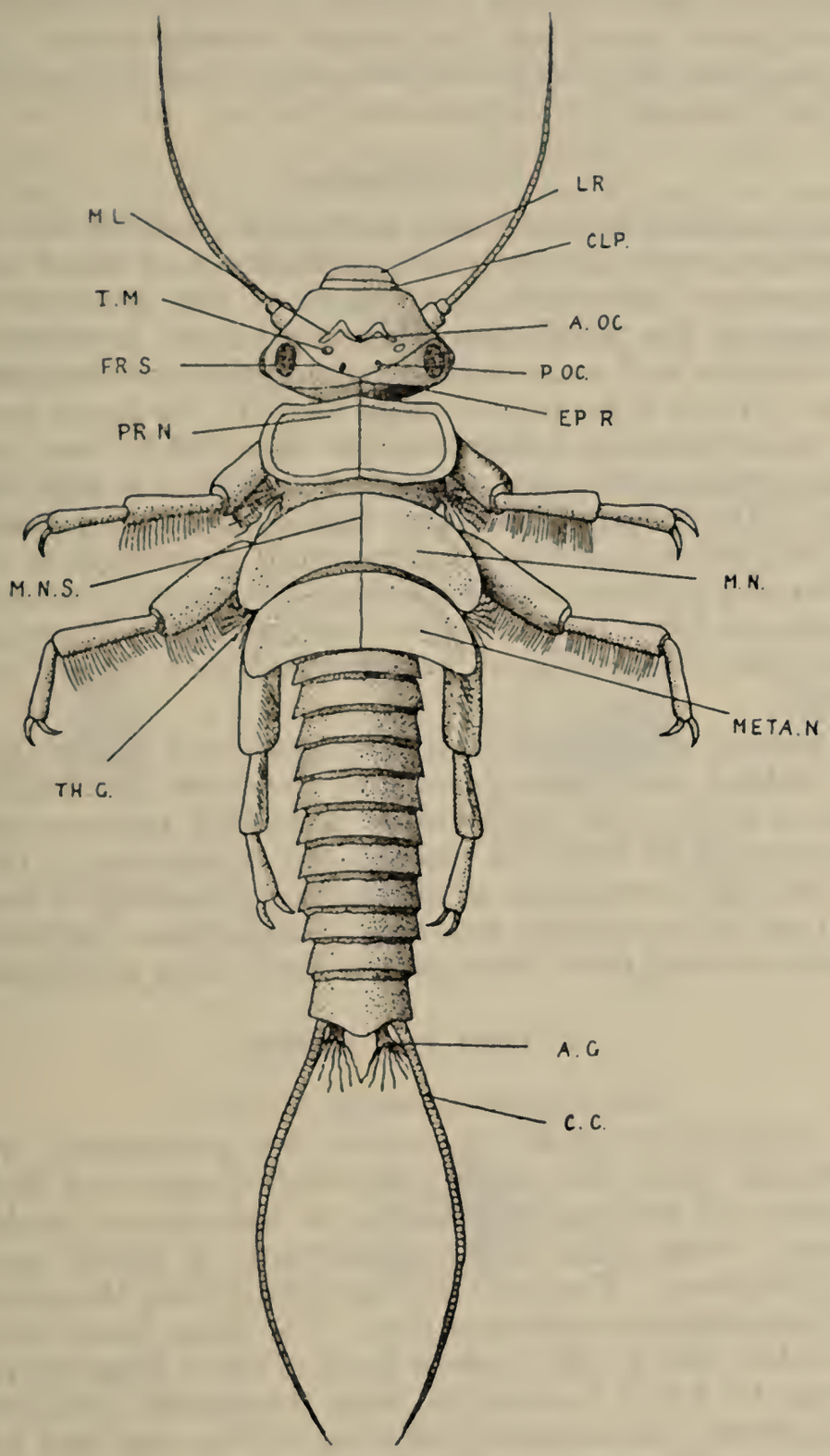

Fig. 1.—Dorsal View of Nymph of *Perla cephalotes*. A.G., anal gill; A.OC., anterior ocellus; CLP., clypeus; C.C., caudal cercus; EP.R., epicranial ridge; FR.S., frontal suture; LR., labrum; M.L., m-shaped line; M.N.S., mesonotal suture; META. N., metanotum; M.N., mesonotum; PR. N., pronotum; P.OC., posterior ocellus; TH. G., thoracic gill; T.M., tentorial macula.

A study of the functional morphology of the nymph and adult of a common stone-fly would, therefore, fill a gap in existing knowledge and serve as a basis for future investigations. It is for this reason that this work has been done and *Perla cephalotes* (Curtis) has been selected for the study.

(2) Techniques

In studying the head and neck of *Perla cephalotes,* live nymphs and adults, as well as preserved specimens and those boiled in 20% potassium hydroxide, were used. The general external morphology of the head was studied and the positions of the various sclerites and sutures determined from microscopical preparations. Whole mounts have been made of the heads and of the various mouthparts and diagrams of these have been prepared from microprojections in an endeavour to obtain a high degree of accuracy. The internal anatomy has been studied from serial sections of Zenker & Bouin fixed material embedded in celloidin or paraffin wax and stained with Erhlich's haematoxylin and eosin. These sections have been used to make reconstructions and the diagrams thus obtained have been checked with the aid of microdissections.

The feeding behaviour of the nymphs and adults has been studied under a binocular microscope, the stone flies having been starved for some days previously. A special perspex container was constructed in order to restrict the movement of the stone flies, so that the movements of the mouthparts could be seen more easily. Low light intensity was used during these observations as the animals showed little inclination to feed when well illuminated.

(3) Third Year Nymphs

(a) *General external features*

The nymphs of *Perla cephalotes* are predacious, living in rapid streams, where the bed is composed of large rock fragments. The nymphs are adapted to this type of habitat and mode of life, by having a wide head and thorax, both of which are dorsoventrally flattened. The head is prognathous with the mouthparts directed forwards for capturing prey. The frons bears three ocelli (fig. 1: A. OC. and P. OC.) just in front of the Y-shaped epicranial suture (fig. 1: FR. S.), while the large compound eyes are dorsolaterally placed. Immediately in front of the eyes and lateral in position are the forwardly-directed antennae.

In the thorax, the pro-, meso-, and meta-nota are expanded to form lateral flanges, which hide the pleura in dorsal view. Each of the laterally-directed legs is composed of a coxa, trochanter, femur, tibia and a three-segmented tarsus, while distally the leg bears a pair of long claws, which are used to cling to the sub-

This paper comprised the substance of a thesis for the M.Sc. degree at the University of Manchester.

stratum. Unlike the head and thorax, the abdomen has a cylindrical form and is composed of ten segments, of which only the first two are divided into terga and sterna. The terminal segment bears postero-laterally two long, many-segmented cerci, between which lie medially two subanal plates or paraproets. These plates each contain a bunch of filamentous gills. Similar tufts of gills—pleural gills—occur ventrally, one on each side, between the thoracic segments, between the prothorax and the neck and between the meta-thorax and the first abdominal segment. Each gill tuft is divided into two parts—one part being above the coxa while the other occurs on the intersegmental membrane immediately posterior to it.

(b) *External morphology of the head*

The head of *Perla cephalotes* differs notably from the definitive type of insect head as envisaged by Snodgrass (1928,

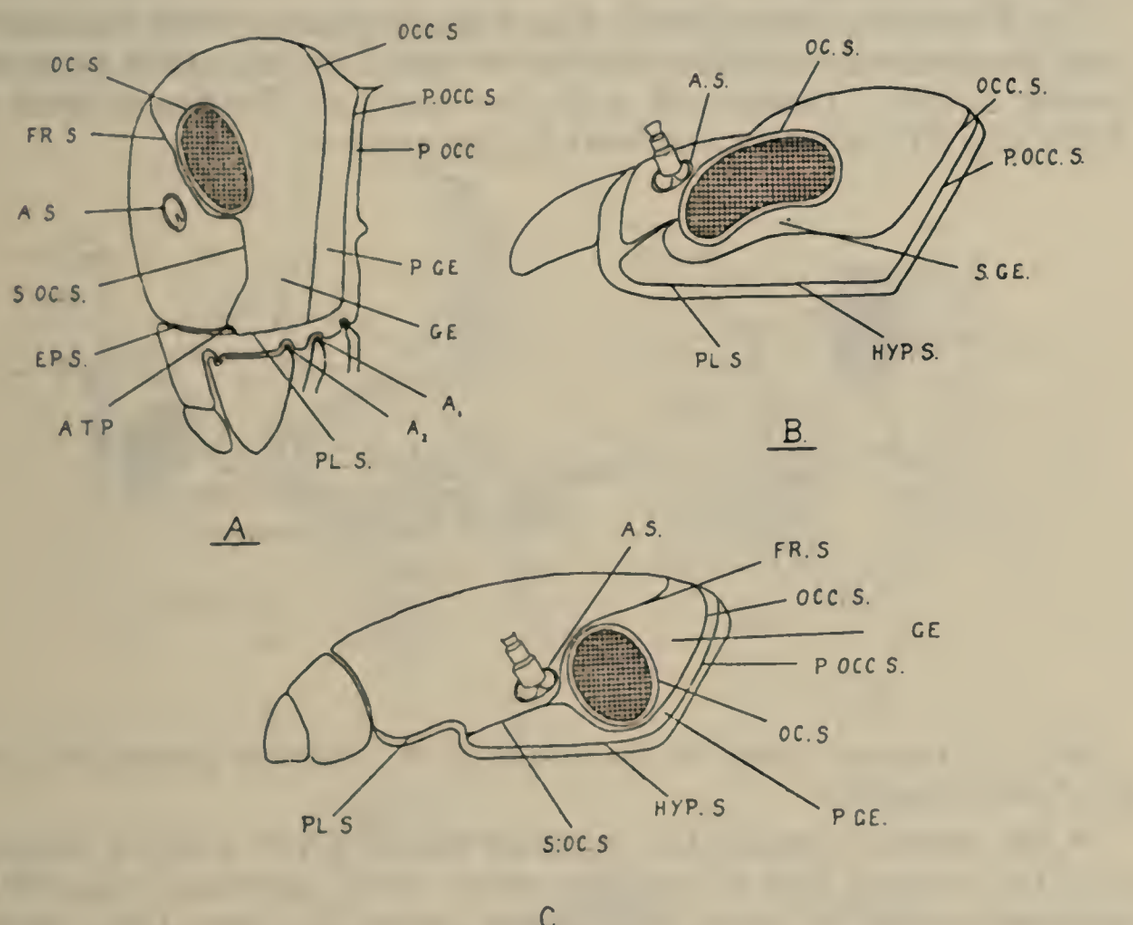

Fig. 2.—Lateral view of the heads of A, generalised insect head (after Snodgrass, 1935); B, *Forficula auricularia* (after Popham, 1959); and C, *Perla cephalotes*.

A.S., antennal suture; A.T.P., anterior tentorial pit; A_1, articulation of maxilla; A_2, articulation of mandible; EP. S., epistomal suture; FR.S., frontal suture; GE., gena; HYP.S., hypostomal suture; OC.S., ocular suture; OCC.S., occipital suture; P.GE., post gena; P.OCC., post occiput; P.OCC.S., post occipital suture; PL.S., pleurostomal suture; S.GE., sub gena; S.OC.S., sub-ocular suture.

1935). The head is prognathous and dorso-ventrally flattened. Assuming the hypognathous type of head to be the primitive condition among the Pterygota, as Snodgrass suggests, prognathism in *Perla cephalotes* seems to have been achieved by changes both in the proportions and relative positions of the constituent parts.

Compared with the head of *Locusta* (fig. 3 A) as typifying the definitive hypognathous type, that of *Perla cephalotes* has become prognathous by a shortening of the frons-epicranial region, a modification which causes the facial aspect to become directed dorsally. The downward and backward migration of the eyes is associated with a great reduction in the size and extent of the genae, each of which becomes reduced to a narrow L-shaped sclerite, which bends forwards under the eyes (fig. 3 B: GE.). Ventrally, the genae are limited by the occipital suture (fig. 3 B: OCC.S.) which appears to become continuous with the epicranial suture in this region.

In *Forficula auricularia* L. (fig. 2 B), Popham (1959) has shown that the genae are dilated and the occipital suture arises from the ocular suture. Compared with the head of *Forficula,* that of *Perla* (fig 2 C) is less specialised in this respect.

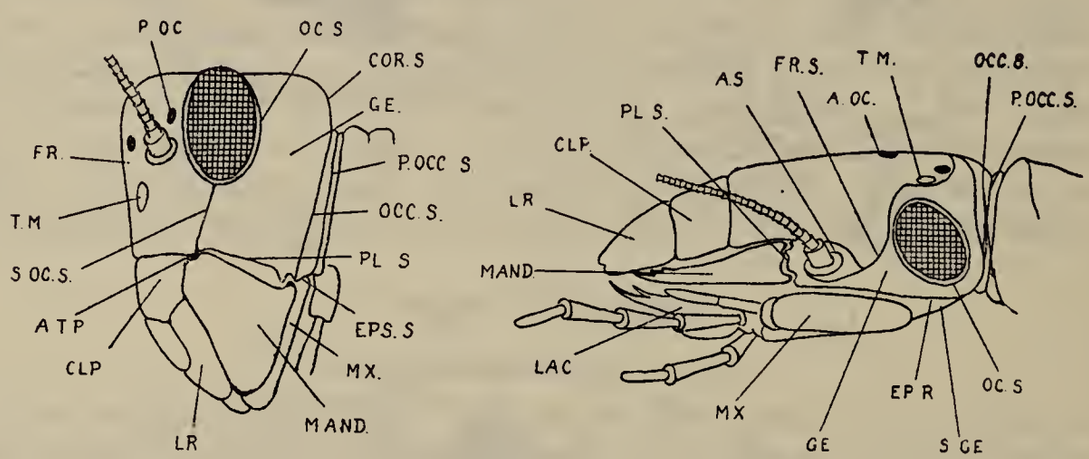

Fig. 3.—Lateral views of the heads of A: *Locusta migratoria,* and B: *Perla cephalotes.*

A.OC., anterior ocellus; A.S., antennal suture; A.T.P., anterior tentorial pit; CLP., clypeus; COR.S., coronary suture; EP.R., epicranial ridge; EP.S., epistomal suture; FR., frons; FR.S., frontal suture; GE., gena; LAC., lacinia; LR., labrum; MAND., mandible; MX., maxilla; OCC.S., occipital suture; OC.S., ocular suture; PL.S., pleurostomal suture; P.OC., posterior ocellus; P.OCC.S., post occipital suture; S.GE., subgena; S.OC.S., subocular suture; T.M., tentorial macula.

This reduction and flexion of the genae in the head of *Perla* have resulted in the mandibles and maxillae being directed forward and thus able to move in a horizontal plane. Dorso-ventral flattening of the head is also associated with the reduction in

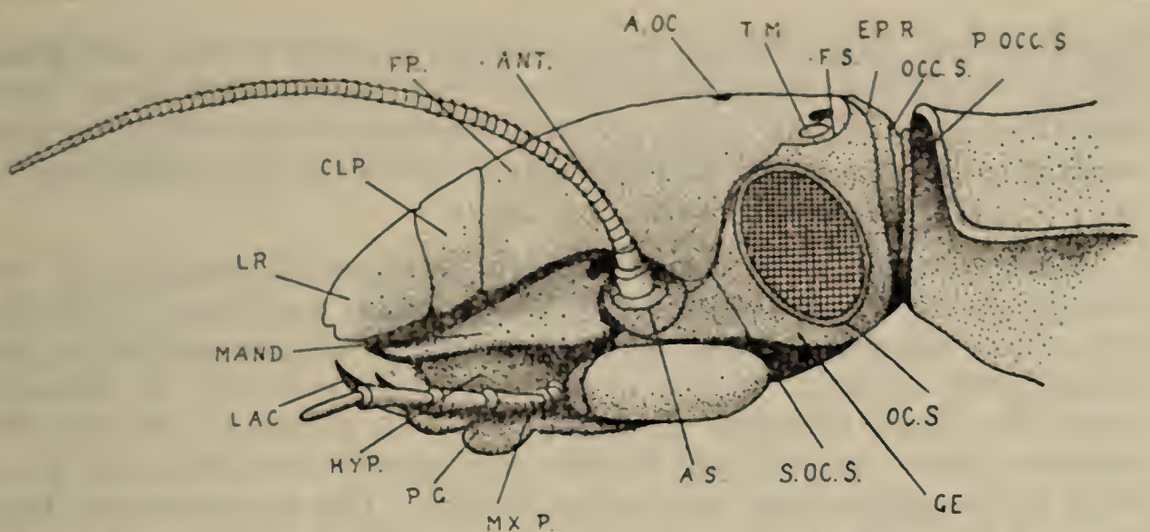

Fig. 4.—Lateral view of the head of *Perla cephalotes*.

A.OC., anterior ocellus; ANT., antenna; A.S., antennal suture; CLP., clypeus; EP.R., epicranial ridge; FR., frons; F.S., frontal suture; GE., gena; HYP., hypopharynx; LAC., lacinia; LR., labrum; MAND., mandible; MX.P., maxillary palp; OCC.S., occipital suture; OC.S., ocular suture; P.G., paraglossa; P. OCC. S., post occipital suture; S. OC. S., sub-ocular suture; T.M., tentorial macula.

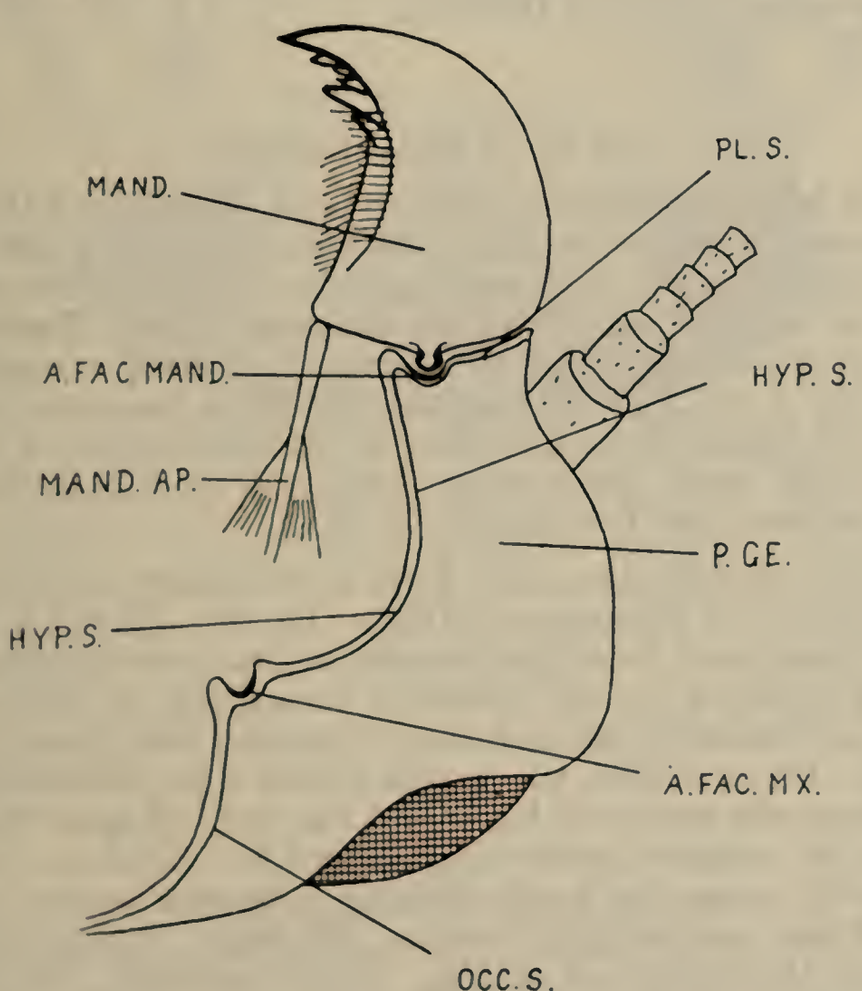

Fig. 5.—Ventral aspect of left half of cranium of *Perla cephalotes* to illustrate the articulating facets of mandible and maxilla.

A.FAC.MAND., articulating facet of mandible; A.FAC.MX., articulating facet maxilla; HYP. S., hypostomal suture; MAND., mandible; MAND. AP., mandibular apodeme; OCC.S., occipital suture; PGE., post gena; PL. S., pleurostomal suture.

length of the pleurostomal suture—that portion of the sub-genal suture, which lies immediately above the mandibular base. The mandibular base has thus become shortened, the rotating axis coming to lie in a plane at right angles to the longitudinal axis of the body (figs. 3, 4: MAND.).

Most significant of these relative changes of position of the various parts of the cranium is that of the antennae. In the hypognathous generalised type of insect head the antennae are immediately anterior to the eyes and would come to lie dorsally when the head becomes prognathous. In *Perla cephalotes* the antennae have moved downwards and partly forwards and have come to lie against the sub-ocular suture. The antennae are thus directed forwards and lie in a horizontal plane with the rest of the body (fig. 4: ANT.).

The change from a hypognathous to a prognathous condition is associated with the ventral side of the head becoming elongated, especially in the region between the mandibular articulating facets and the bases of the maxillae. This hypostomal elongation of the head capsule gives the maxillae a greater degree of mobility as prehensile organs (fig. 5: HYP.S.).

(c) *The Cranial Capsule*

In the head capsule the sclerites tend to fuse and the frontal and coronary sutures are incomplete and in places can only be traced with difficulty. Along the anterior margin of the labrum is a series of forward and medially directed setae. The posterior margin of the labrum can be retracted under the membranous clypeus (fig. 6: CLP.). Behind the clypeus is the frons (fig. 4, 6: FR.), which forms the major part of the dorsal wall of the head capsule. The frons bears three ocelli, the median ocellus being anterior to the other two (fig. 6: P. OC.).

At the posterior edge of the frons is the frontal suture (or post frontal suture of Snodgrass (1935) (fig. 6: FR.S.). Running medially backward from this suture to the post-occipital suture (fig. 6: P. OCC. S.) is the coronary suture (fig. 6: C. S.). The frontal and coronary join to form a Y-shaped fork directly behind the ocelli. On each side, the frontal suture runs downwards laterally between the antennal bases and the eye. Behind the frontal suture is the occipital suture (figs. 3 and 6: OCC.S.). This runs transversely across the head, defining a narrow occiput between itself and the post-occipital suture. Medially, this occiput is cut in half by the epicranial suture. Ventro-laterally, the occipital suture bends forwards under the ocular suture (fig. 4: OC. S.) to cut off, below, a post-genal area above the articulating bases of the maxillae. In this sub-ocular region, the occipital suture becomes continuous with the epicranial ridge (figs. 6 and 7: EP. R.), which runs beneath the bases of the antennal and ocular sutures. The

post-occipital suture exists as a transverse groove around the posterior margin of the head. Posteriorly, it demarks off a post-occipital arch, which surrounds the foramen magnum. Attached to the post-occiput is the cervical membrane.

Compared with the head of *Locusta,* the occiput and genae of the nymphal head of *Perla* are short and reduced in length. The functional significance of this will be discussed later.

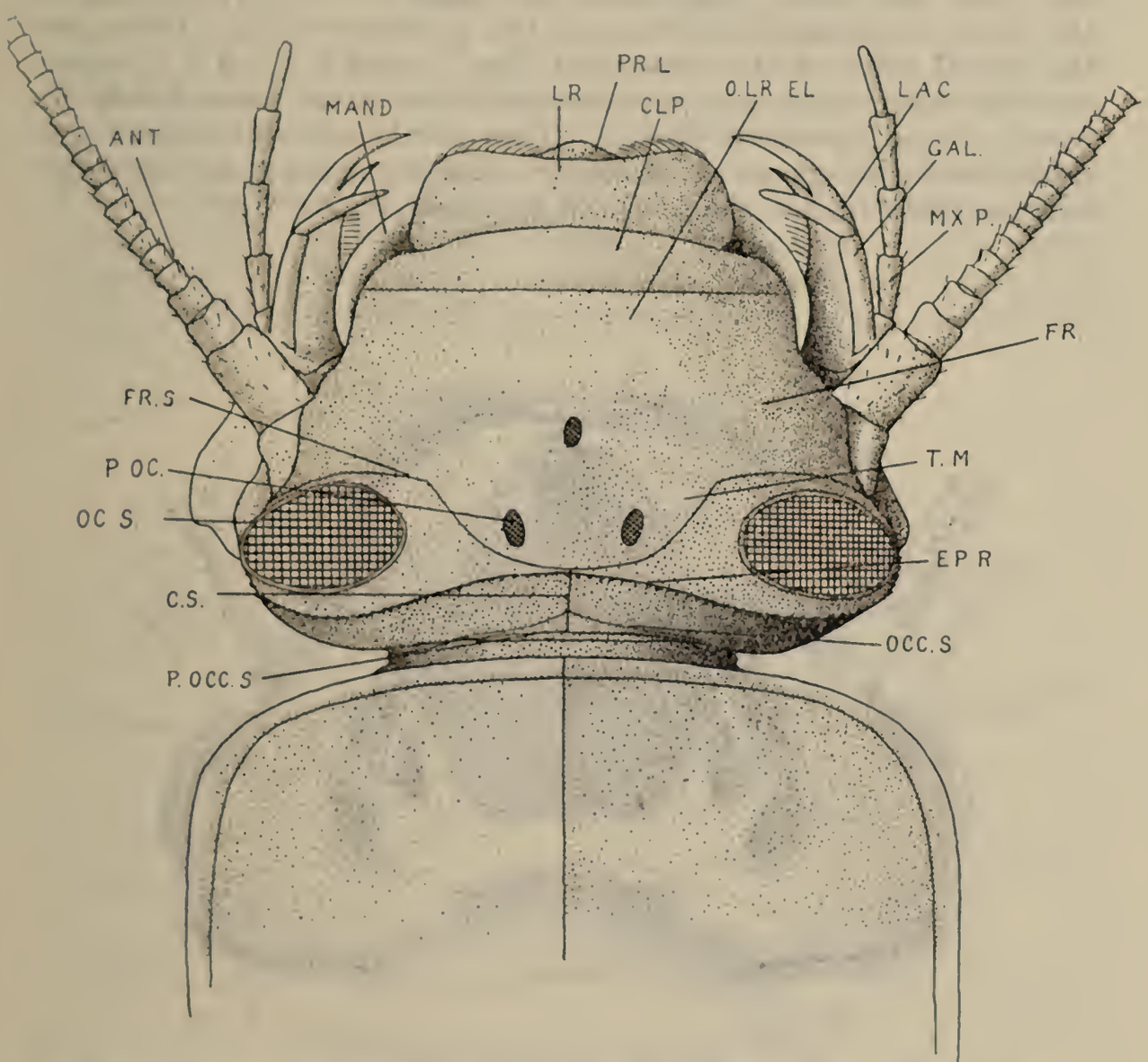

Fig. 6.—Dorsal view of the head of *Perla cephalotes.*

ANT., antenna; CLP., clypeus; C.S., coronary suture; EP.R., epicranial ridge; FR., frons; FR.S., frontal suture; GAL., galea; LAC., lacinia; LR., labrum; MAND., mandible; MX. P., maxillary palp; OC. S., ocular suture; OCC.S., occipital suture; O.LR.EL., origin of labral elevator; PR.L., prelabrum; P.OC., posterior ocellus; P. OCC. S., post occipital suture; T.M., tentorial macula.

(d) *The Tentorium*

The tentorium of *Perla cephalotes* resembles that of the primitive type of insect being similar to the π shaped structure described by Snodgrass (1935). It consists of a flat ventral plate over the posterior part of the labium, which is laterally attached to the ventral ends of the post occipital arch. The posterior arms of the tentorium are extremely short, but the tentorial body is extended dorso-laterally forwards to form on each side an anterior arm (figs. 7 and 8: A.A.T.). These arms are formed from invaginations of the epistomal suture. From the dorsal surface of these anterior arms two narrow branches are given off dorsally, one from each arm, and become attached to the hypodermis of the frons immediately in front of the posterior ocelli. These are the dorsal arms of the tentorium (figs. 7 and 8: D.A.T.), which become attached to the hypodermis of the frons immediately in front of the posterior ocelli. The points of attachment are indicated by the presence of two pit-like depressions on the outer surface of the frons—the tentorial maculae (fig. 6: T.M.).

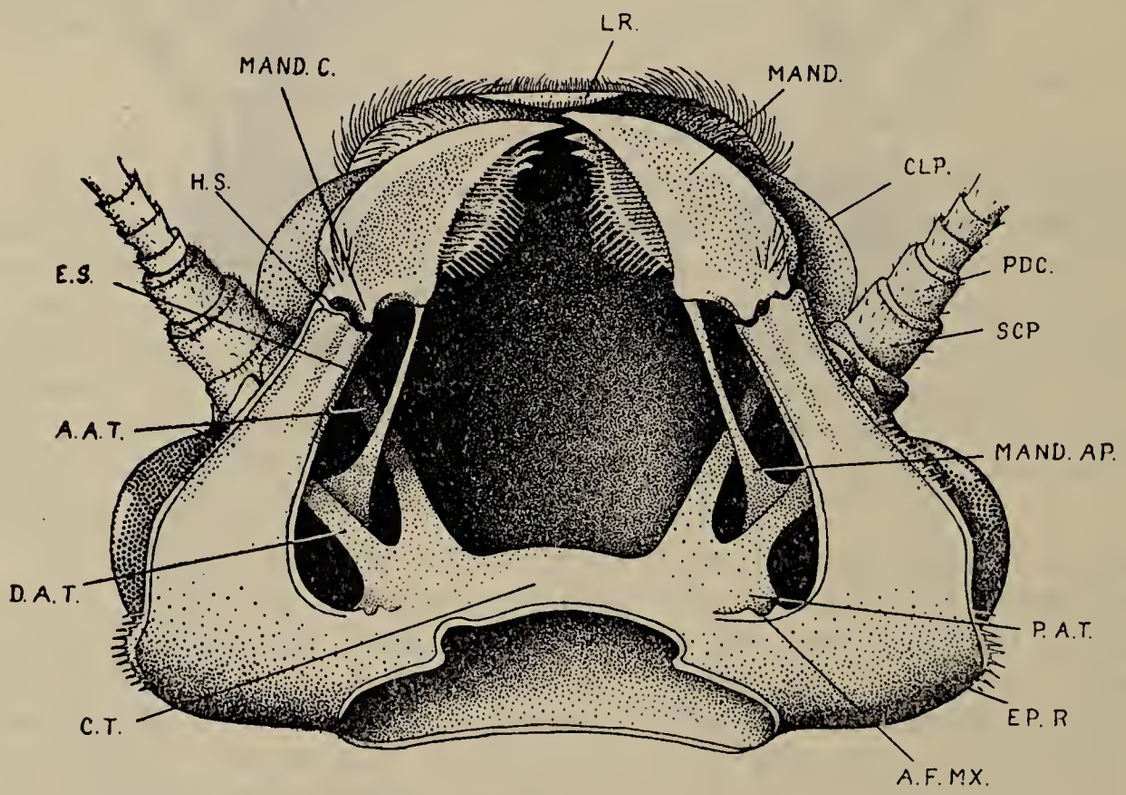

Fig. 7.—Ventral view of the head of *Perla cephalotes* with labium and maxillae removed.

A.A.T., anterior arm of tentorium; A.F.MX., articulating facet of maxilla; CLP., clypeus; C.T., tentorial body; D.A.T., dorsal arm of tentorium; EP.R., epicranial ridge; E.S., epistomal suture; H.S., hypostomal suture; LR., labrum; MAND., mandible; MAND. AP., mandibular apodeme; MAND.C., mandibular condyle; P.A.T., posterior arm of tentorium; PDC., pedicel; SCP., scape.

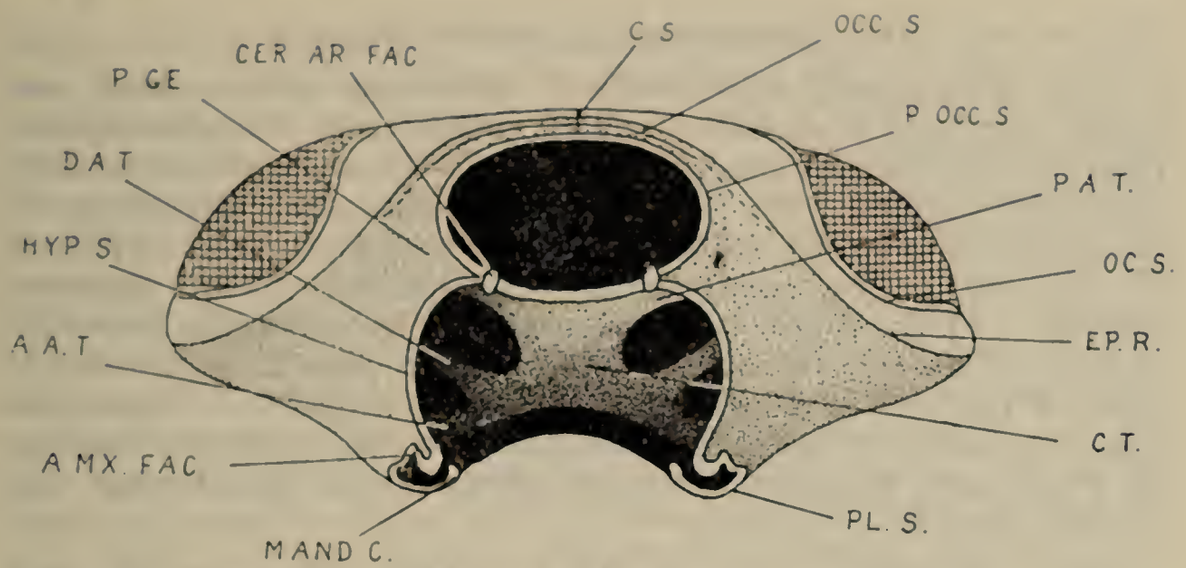

Fig. 8.—Posterior view of head of *Perla cephalotes*.

A.A.T., anterior arm of tentorium; A.MX.FAC., articulating facet of maxilla; C.S., coronary suture; CER.AR.FAC., cervical articulating facet; C.T., tentorial body; D.A.T., dorsal arm of tentorium; EP.R., epicranial ridge; HYP.S., hypostomal suture; MAND.C., mandibular condyle; OCC.S., occipital suture; OC.S., ocular suture; P.A.T., posterior arm of tentorium; P.GE., post gena; P.OCC. S., post-occipital suture; PL.S., pleurostomal suture.

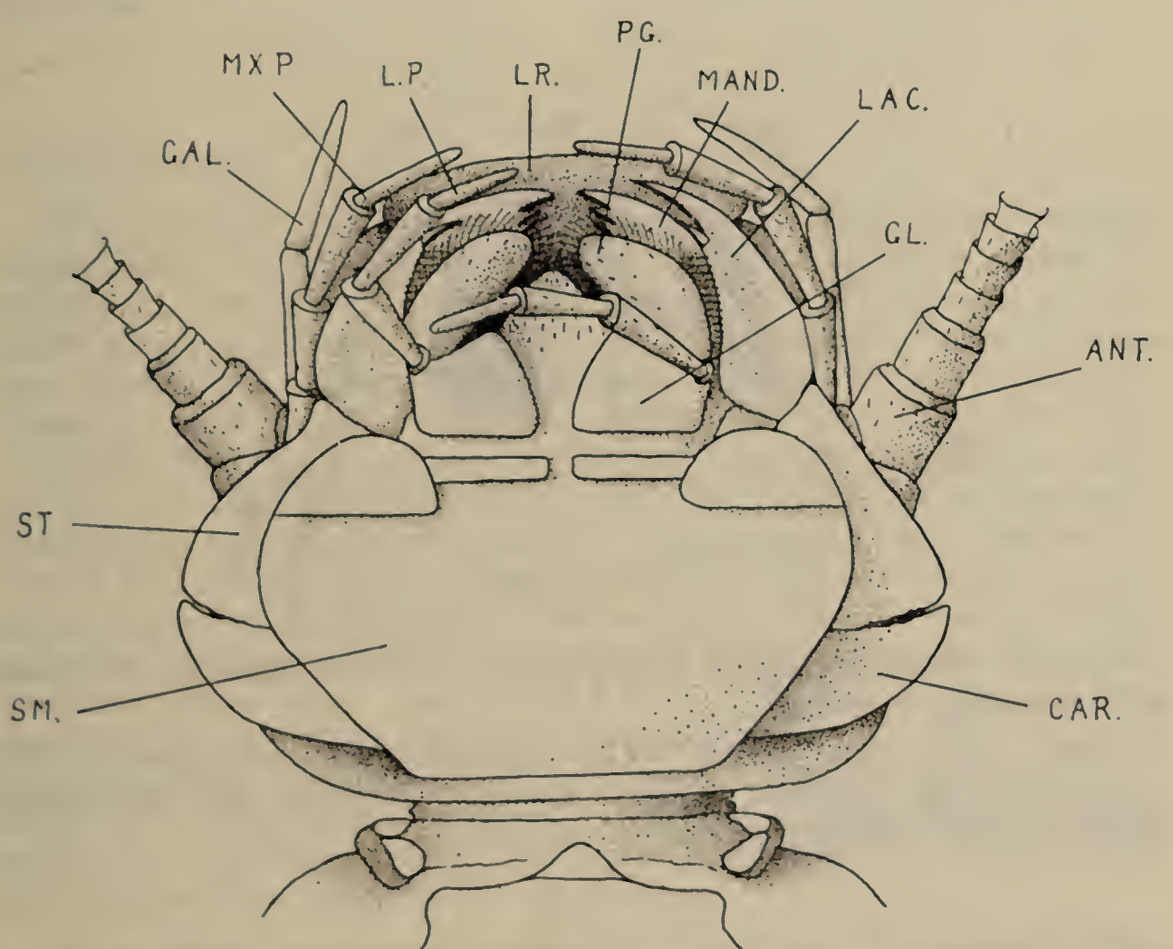

Fig. 9.—Ventral view of the head of *Perla cephalotes*.

ANT., antenna; CAR., cardo; GAL., galea; GL., glossa; LAC., lacinia; LR., labrum; LP., labial palp; MAND., mandible; MX.P., maxillary palp; PG., paraglossa; SM., submentum; ST., stipes.

(e) *Morphology of the Mouthparts*

The pronounced dorso-ventral flattening of the head and thorax of *Perla cephalotes* is also reflected in the mouthparts. They are directed forwards and all move within confined, narrow, horizontal planes. To increase the mechanical advantage of mouthpart movement within this restricted plane, it is necessary for the articulating facets of these appendages to be displaced laterally. This is found to be the case. In addition, the genae are expanded laterally beneath and behind the eyes to form a broad base for the points of articulation of the cardines. These limb segments are also extended laterally and the posterior ends of the stipes are, therefore, situated lateral to the genal ridge (fig. 9: CAR. and ST.).

The articulating bases of the mandibles are, however, very narrow, and their movements would be quite insecure and unstable if there were not some protective mechanism to support them. This is provided by the broad base and expanded lateral margins of the submentum (fig. 9: SM.), which overlap the bases of the maxillae, enclosing them in a protective groove and restricting their movement to the horizontal plane.

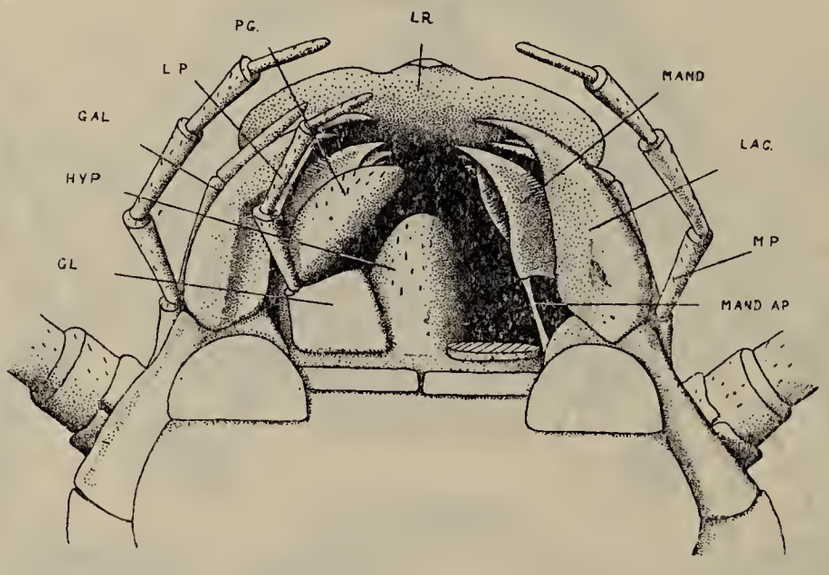

Fig. 10.—Ventral view of mouthparts of *Perla cephalotes*, left glossa and paraglossa removed.

GAL., galea; GL., glossa; HYP., hypopharynx; LAC., lacinia; L.P., labial palp; LR., labrum; MAND., mandible; MAND. AP., mandibular apodeme; M.P., maxillary palp; PG. paraglossa.

(i) *The Labrum*

The labrum is broader than long and is attached by arthrodial membrane to the underside of the anterior margin of the clypeus (figs. 6 and 10: LR.). Along its anterior margin, the labrum

bears a row of fine hairs. Protruding medially under this anterior margin is a cone-shaped lobe or pre-labrum (fig. 6: PR.L.). The ventral surface of the labrum, on either side of this lobe, is covered with setae directed obliquely, medially and backwards towards the pharynx. Two small muscles, the cibarial dilator muscles (fig. 11: CIB., DIL.), which originate on the loop of cuticle forming the posterior margin of the labrum are inserted on the ventral surface of the labral lobe. Contraction of these muscles elevates the base of the labral lobe, thereby extending slightly a greatly reduced cibarium. The lateral margins of the loop of cuticle bordering the posterior margin of the labrum are directed downwards, to form two rod-shaped tormae (fig. 19: LR. TOR.), which act as the points of insertion of the labral depressor muscles (figs. 11 and 19: LR. DEP.). These muscles run postero-laterally and find their origins on the frons slightly mesad of the antennal bases (Fig. 6: O. LR. EL.).

The labrum is elevated by two muscles, the labral elevators (fig. 11 and 19: LR. EL.), which originate medially on the frons directly in front of the anterior ocellus and are inserted dorsally on the posterior cuticular ridge of the labrum. The origins of these muscles are responsible for the two inner limbs of the M line of the frons.

(ii) *The Mandibles*

The mandibles are heavily sclerotised and dorso-ventrally compressed, except towards the posterior end where there is a thickened base. The ventral surface of each is concave, so that when these appendages meet, a cavity is formed between them into which fits the anterior dorsal surface of the hypopharynx. Distally, each mandible bears six teeth, those on the right mandible forming a cutting edge that fits between similar teeth on the left mandible during mandibular closure. Immediately behind the posterior teeth are two longitudinal rows of setae (fig. 12: MAND. S.), which run backwards to the point of attachment of the mandibular adductor muscles (fig. 7: MAND. AP.). These setae are directed postero-medially and help to hold the food while the mandibles close. They also help to prevent freshly-cut food particles from falling out of the cibarial cavity and assist in brushing them towards the oesophagus. Between these rows of setae is a longitudinal groove. On the dorsal aspect of each mandible is another line of fine hairs, also medially directed and running parallel to the other two ridges.

Mandibular movement is out of phase with that of the hypopharynx. As the mandibles open the hypopharynx is pushed upwards between the rows of mandibular setae, thus ensuring that particles of food, cut from the prey by the scissor-like action of the mandibles are pushed back into the oesophagus.

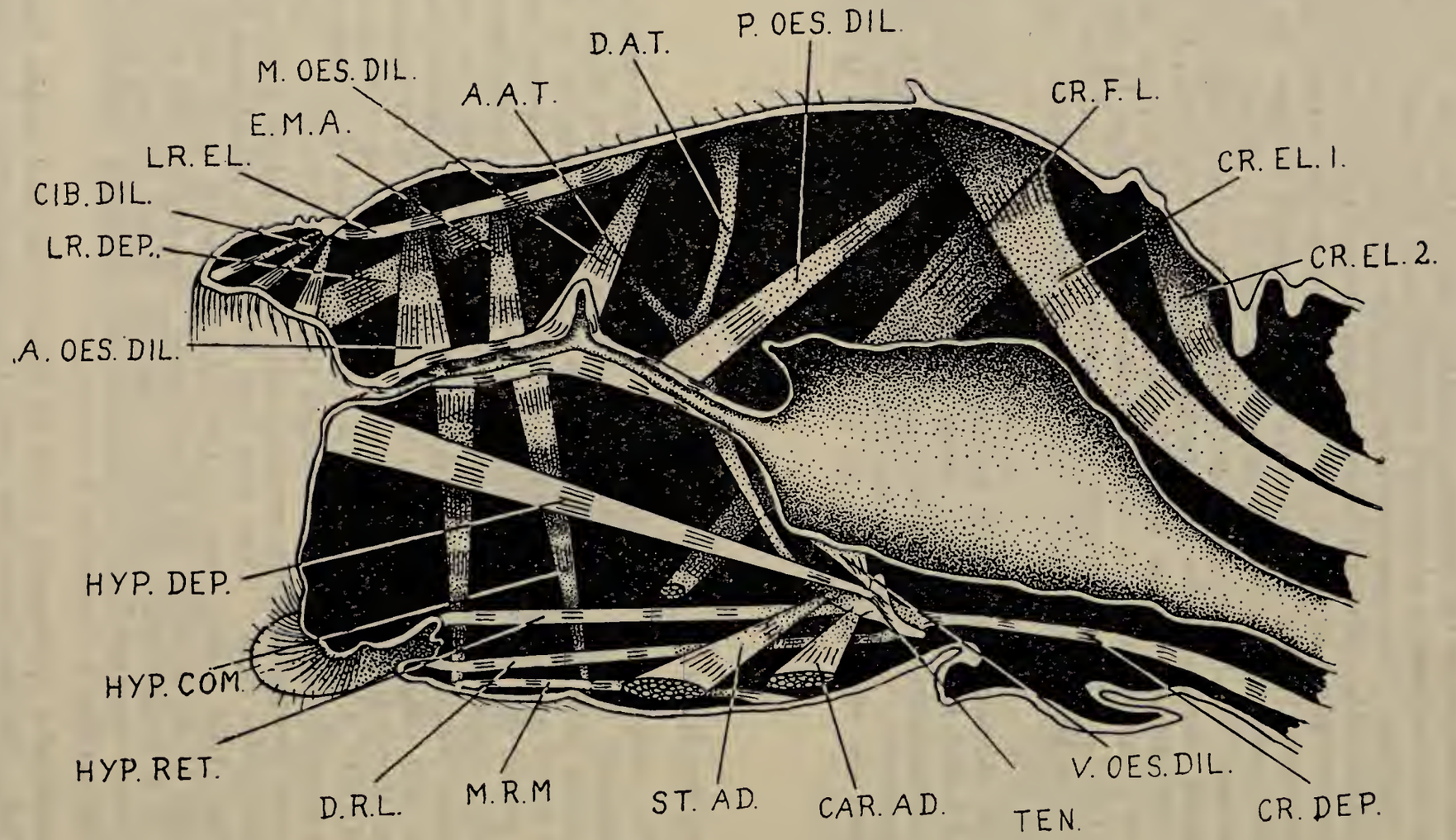

FIGURE 11 — See page opposite.

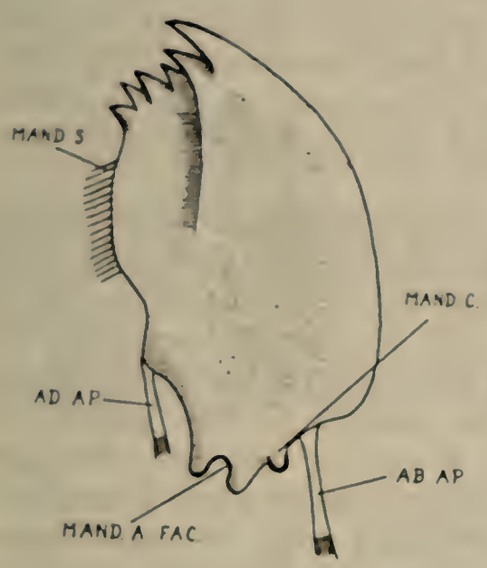

Fig. 12

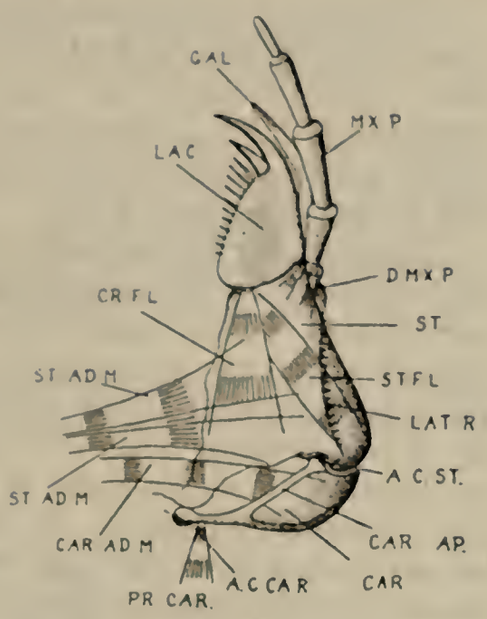

Fig. 13

Fig. 12.—Ventral view of left mandible of *Perla cephalotes*.

AB. AP., abductor apodeme; AD. AP., adductor apodeme; MAND. A. FAC., articulating facet of mandible; MAND. C., mandibular condyle; MAND. S., mandibular setae.

Fig. 13.—Ventral view of left maxilla.

A.C. CAR., articulating condyle of cardo; A.C. ST., articulating condyle of stipes; CAR., cardo; CAR. AP., apodeme of cardo; CAR. AD. M., adductor muscle of cardo; CR. F.L., cranial flexor of lacinia; D. MX. P., depressor of maxillary palp; GAL., galea; LAC. lacinia; LAT. R., lateral ridge; M.P., maxillary palp; PR. CAR., protractor of cardo; ST., stipes; ST. AD. M., stipes adductor muscles; ST. F.L., stipital flexor of lacinia.

Fig. 11.—Sagittal half of the head of *Perla cephalotes* to illustrate cranial musculature.

A.A.T., anterior arm of tentorium; A. OES. DIL., anterior oesophageal dilator; CAR. AD., adductor of cardo; CIB. DIL., cibarial dilator; CR. DEP., cranial depressor; CR. EL. 1, cranial elevator 1; CR. EL. 2, cranial elevator 2; CR. F. L., cranial flexor of lacinia; D.A.T., dorsal arm of tentorium; D.R.L., distal retractor of labium; E.M.A., elevator of mouth angle; HYP. COM., hypopharyngeal compressor; HYP. DEP., hypopharyngeal depressor; HYP. RET., hypopharyngeal retractor; LR. EL., labral elevator; LR. DEP., labral depressor; M. OES. DIL., medial oesophageal dilator; M.R.M., mental retractor muscle; P. OES. DIL., posterior oesophageal dilator; ST. AD., stipes adductor; TEN., tentorium; V. OES. DIL., ventral oesphageal dilator.

Ventrally, each mandible articulates by means of a knob-like condyle (fig. 12: MAND. C.) with a depression in the post-genal rim, while dorsally it bears a cup-shaped depression (fig. 12: MAND. A. FAC.), which articulates with the head at the junction of the anterior arm of the tentorium and the epistomal suture near the anterior tentorial pit.

Mandibular movement is affected by powerful muscles which are attached to the posterior wall of the cranium, to the genae and post-genae. The mandibles are opened by the contraction of a pair of abductor muscles (fig. 14: M. AB. M.), which originate on the posterior wall of the cranium, and are inserted by an apodeme on the posterior rim of the mandible lateral to the points of articulation. Adduction is effect by a similar though stronger pair of muscles (fig. 14: M.AD.M.). The origins of these mandibular adductor muscles are widely distributed over the epicranial plates and the genae. The muscle fibres are attached anteriorly to an apodeme which is inserted on the posterior face of the mandible mesad of the points of articulation. These two sets of muscles, both adductor and abductor, are situated ventral to the anterior arm of the tentorium.

(iii) *The Maxillae*

On each side of the head a maxilla is situated ventral to the mandible. Each maxilla is composed of a basal element comprising a cardo and stipes, the latter giving rise distally to a five-segmented palp, a galea and a lacinia. Each maxilla lies in a longitudinal groove formed between a lateral expansion of the genae dorsally and an expansion of the submentum centrally. This groove confines maxillary movement to the horizontal plane. Like the mandibles, all maxillary parts are dorso-ventrally compressed, the laciniae having a concave ventral surface. The cavity formed between the closed maxillae merges with that of the mandibles forming the roof of the cibarial cavity (fig. 10).

The cardo is a rather thick triangular sclerite articulating dorsally with the cranium by means of a spherical condyle (fig. 13: A.C. CAR.), while ventrally it is connected by arthrodial membrane to the base of the submentum. The articulating condyle of the cardo fits into a cavity on the posterior margin of the post-gena (fig. 7: A.F. MX). Internally the cardo is strengthened by two struts, one running from the articulating condyle of the cardo along its inner wall to the articulating base of the stipes, the other an internal apodeme running transversely across the cardo from its basal condyle to that on which the stipes articulates (fig. 13: CAR. AP.).

The stipes is a long, narrow sclerite divided dorsally by a longitudinal suture into a palpifer bearing a five-segmented palp and a narrow lightly sclerotised galea. Posteriorly it articulates with the cardo which antero-laterally bears a condyle (fig. 13: A.C. ST.). The dorsal median edges of the cardo and stipes are joined by arthrodial membrane to the underside of the head

capsule, while the ventral median edges are similarly connected with the lateral margins of the labium. This means that the haemocoel of the maxilla is confluent with the haemocoel of the head.

Anteriorly the lacinia is articulated on the stipes. The lacinia is heavily sclerotised and distally bears a pair of sharp, medially-directed teeth, the posterior one of which is hinged to the inner lacinial wall. Medially each lacinia tapers to a sharp medial edge, which bears a single row of orally-directed fine setae (fig. 13: LAC.).

Maxillary musculature and movement are more complex than those of the mandibles. Though the maxillary movements are

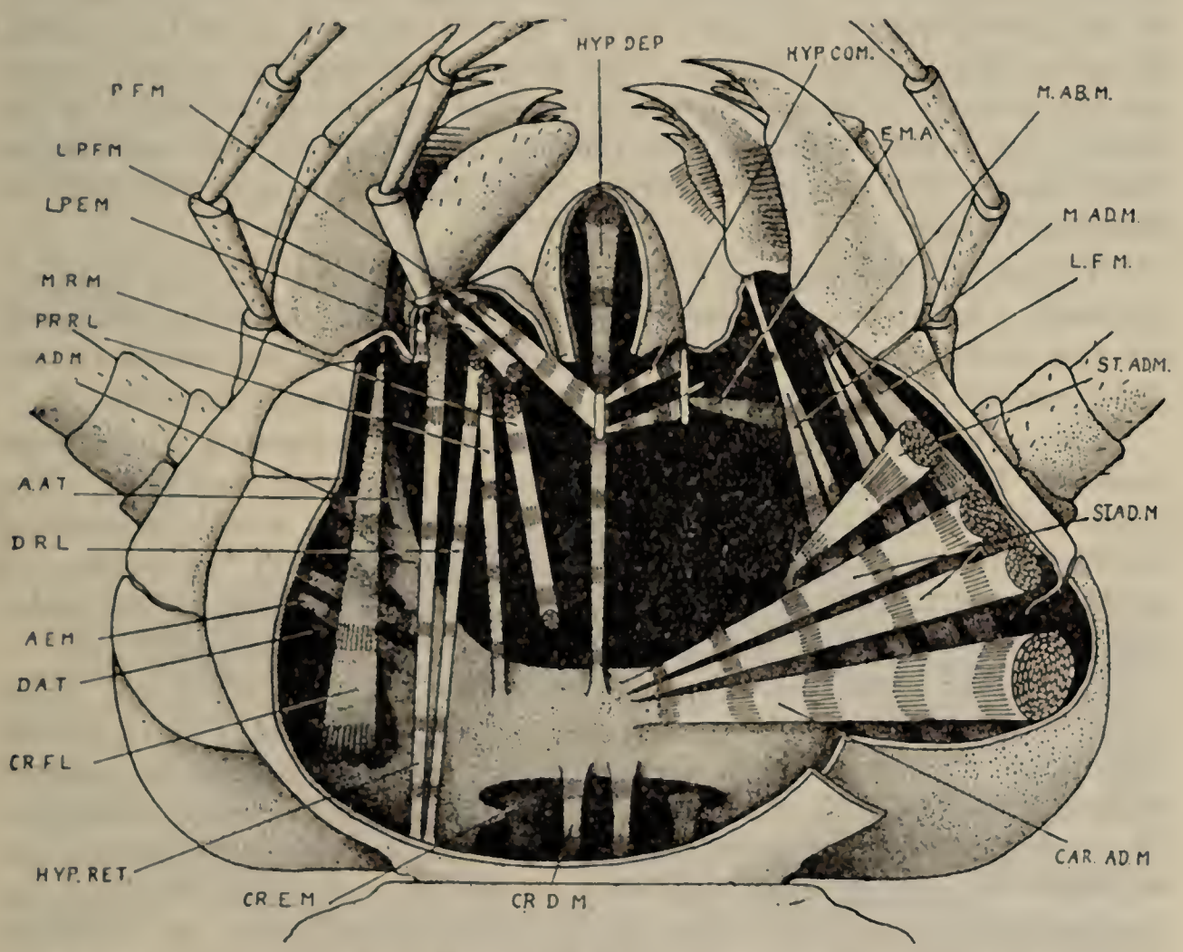

Fig. 14.—Ventral view of head of *P. cephalotes* with part of labium removed to exhibit musculature of mouthparts.

A.A.T., anterior arm of tentorium; A.D.M., antennal depressor muscle; A.E.M., antennal elevator muscle; CAR.AD.M., adductor muscle of cardo; CR.D.M., cranial depressor muscle; CR.E.M., cranial elevator muscle; CR.F.L., cranial flexor of lacinia; D.A.T., dorsal arm of tentorium; D.R.L., distal retractor of labium; E.M.A., elevator of mouth angle; HYP. COM., compressor of hypopharynx; HYP. DEP., depressor of hypopharynx; HYP. RET., hypopharyngeal retractor; L.F.M., lacinial flexor muscle; L.P.E.M., labial palp elevator muscle; L.P.F.M., labial palp flexor muscle; M. AB.M., mandibular abductor muscle; M.AD.M., mandibular adductor muscle; M.R.M., mental retractor muscle; P.F.M., paraglossal flexor muscle; PR.RL., proximal retractor of labium; ST.AD.M., stipes adductor muscle.

mainly restricted to a horizontal plane, the maxillae are also capable of being extended and retracted. Adduction is effected by the contraction of the cardo adductor muscle (figs. 13 and 14: CAR. AD. M.), which originates laterally on the ventral surface of the tentorial body and is inserted on the posterior wall of the cardo. Contraction of this muscle also causes maxillary extension and the lacinial teeth are, therefore, driven forwards and inwards to meet anterior to the labrum, where they are used to hold the prey in position during feeding. The adductor muscle of the stipes (fig. 14: ST. AD. M.) has three branches. Two of these branches arise on the ventral surface of the tentorial body and the third from the base of the anterior arm of the tentorium. All three branches are inserted on the lateral wall of the stipes next to its lateral ridge (fig. 13: LAT. R.). Contraction of the cranial flexor of the lacinia (fig. 13: CR. F.L.) by a muscle arising on the posterior wall of the gena and inserted on the inner base of the lacinia, not only retracts the maxilla as a whole, but simultaneously flexes the lacinia inwards. The significance of this will be discussed later.

The maxillary palp is a five-jointed structure. At its base are inserted a levator and a depressor muscle, both of which originate on the outer wall of the stipes. All the other segments of the palp, except for the most distal, bear a single flexor muscle.

The galea is a long, cylindrical appendage curved slightly inwards. It is divided into a distal and proximal section. The galea is abducted by the galeal abductor muscle, which is inserted laterally on the base of the galea and originates on the stipes. A galeal flexor muscle is inserted medially on the base of the galea and originates on the wall of the stipes.

One small muscle is responsible for maxillary abduction. This is the promotor muscle of the cardo (fig. 13: PR. CAR), which originates on the lower posterior wall of the gena and is inserted on the posterior wall of the cardo lateral to its articulating condyle. It would appear that abduction of the other maxillary parts, such as those of the galea, palp and stipes is probably effected by haemocoelic fluid pressure, there seemingly being no muscles present to effect these movements.

Retraction of the maxilla as a whole can be brought about by contraction of the cranial flexor of the lacinia (figs. 11, 13: CR. F. L.). This contraction tends to draw the prey against the cutting edge of the mandibles.

(iv) *The Hypopharynx and Salivary Glands*

The hypopharynx is a tongue-like lobe filling most of the cibarial cavity and so shaped that its convex dorsal surface fits into the cavity formed between the closed mandibles and maxillae. Its outer surface is soft and unsclerotised except for a number of supporting rods. The dorsal suspensorial rod (fig. 15: S. SCL.) is

a hoop-like structure running transversely across the hypopharynx. Laterally it becomes partly fused with two short lateral suspensorial rods (fig. 15: A.A.S. SCL.). These rods are parallel with the longitudinal axis of the body and serve for the attachment of hypopharyngeal and mouth angle muscles. A basal rod (fig. 15: B.R.), looping around under the hypopharynx, connects the lateral suspensorial sclerites with a ridge of cuticle formed by an invagination of the prementum.

The hypopharynx is dilated by haemocoelic pressure and raised by the contraction of the elevator of the mouth angle muscles (fig. 15: E.M.A.). These arise on the anterior dorsal wall of the frons and are inserted on the posterior lateral suspensorial sclerite (fig. 15: P.A. S. SCL.). There are two other pairs of muscles, the hypopharyngeal compressor muscles, one inserted on the ventral surface of the posterior lateral suspensorial rods, the other on the anterior, run meso-ventrally and are attached to a sclerotised invagination of the prementum anterior to the ventral salivary cup (fig. 15, H. COM.). These serve, on contraction, to produce a salivary flow from the hypostomal salivary glands by exerting a pressure on the glands and associated ducts.

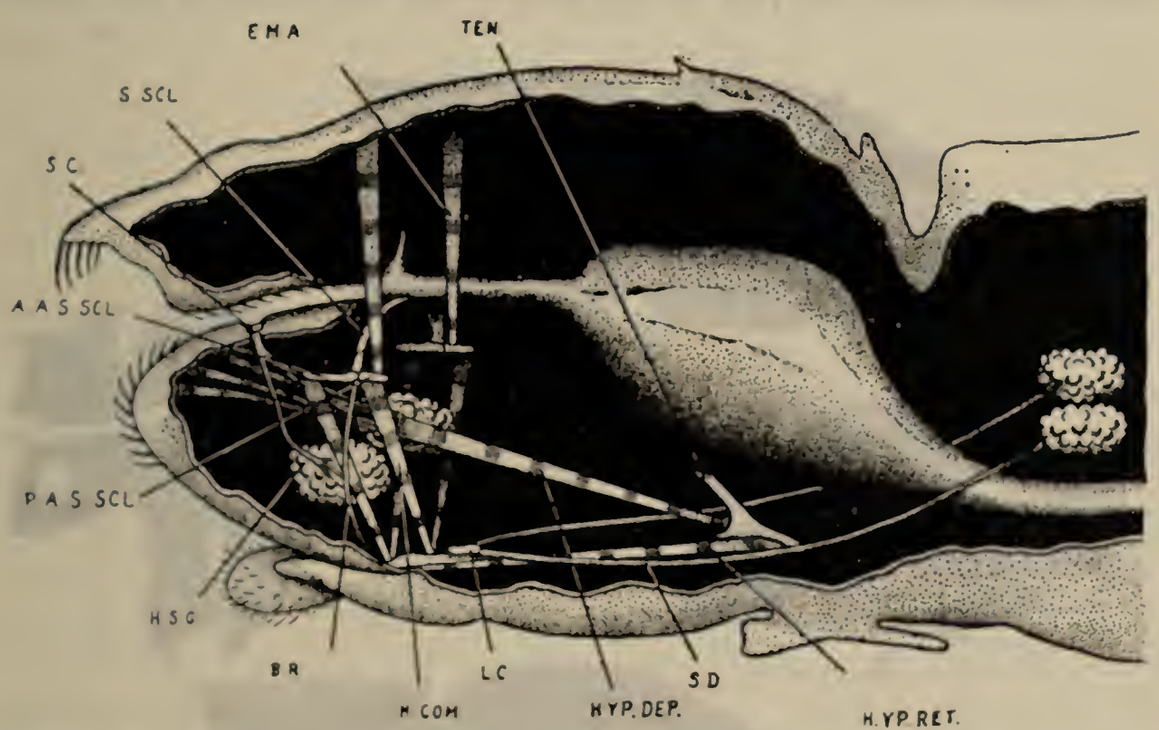

Fig. 15.—Sagittal half of head of *Perla cephalotes* to show musculature of the hypopharynx.

A.A.S.SCL., anterior arm of suspensorial sclerite; B.R., basal rod; E.M.A., elevators of mouth angle; H.COM., hypopharyngeal compressor; HYP. DEP., hypopharyngeal depressor; HYP. RET., hypopharyngeal retractor; H.S.G., hypopharyngeal salivary gland; L.C., labial cup; P.A.S. SCL., posterior arm of suspensorial sclerite; S.C., salivary cup; S.D., salivary duct; S. SCL., suspensorial sclerite; TEN., tentorium.

Hypopharyngeal movement is also effected by three other muscles, namely, a single medial hypopharyngeal depressor muscle, which arises on the ventral surface of the tentorial body and is inserted on the tip of the hypopharynx immediately anterior to the salivary cup (fig. 15: HYP. DEP.) and the retractor muscles of the hypopharynx (figs. 11 and 14: HYP. RET.). On each side, a muscle is attached to the posterior arm of the tentorium and is inserted on the ventral end of the basal rod (fig. 15: B.R.). These muscles depress and retract the hypopharynx, while the laciniae push food particles into the cibarial cavity. Since there are no extensor muscles in the hypopharynx, labial and maxillary palps, glossae or paraglossae, the extension of these mouth parts would appear to be effected by haemocoelic fluid pressure.

In his description of *Nemoura,* Wu (1923) describes only two pairs of salivary glands, one pair in the prothorax and the other in the mesothorax. In *Perla cephalotes,* however, there are three pairs of glands. A single pair of glands, the maxillary glands (fig. 15: H.S.G.), lie in the hypopharyngeal lobe, one on each side. A duct from each of these runs forwards and upwards, fuses with that of the other, and the common duct opens into a small salivary cup on the upper surface of the hypopharynx (fig. 15: S.C.). Two other pairs exist, one pair in the prothorax, the other in the meso-

Fig. 16.—A: Maxillary and labial glands as in many Apterygota. B: Maxillary glands of *Forficula auricularia* (after Popham, 1959). C: Labial glands of cockroach. D: Maxillary and labial glands of *Perla cephalotes.*

thorax. These are usually called the labial glands. Both pairs are lateral to the alimentary canal. The ducts from each of the mesothoracic glands run forward, fuse with those of the prothoracic glands and the common ducts run through the foramen magnum, along the base of the labium and open separately into a cup that lies between the centre of the labium and the base of the hypopharynx (fig. 15: S.D.).

It is of interest to compare the relative positions and to examine the nature of the salivary glands in the Plecoptera, the Dermaptera and the Dictyoptera. Fig. 16A represents the type, from which others may have evolved, where both maxillary and labial glands are present and are quite separate. This represents the condition found among many Apterygote insects, where both maxillary and labial glands are commonly present, as well as in *Perla cephalotes* (fig. 16D). In the cockroach, only the labial glands are represented (fig. 16C), while in the Dermaptera there are two pairs of glands in the head (Popham, 1959) (fig. 16B). Whether these two pairs of glands are maxillary glands or represent maxillary and labial glands, the ducts of which have united, is not clear. Further investigation into the matter might give valuable information.

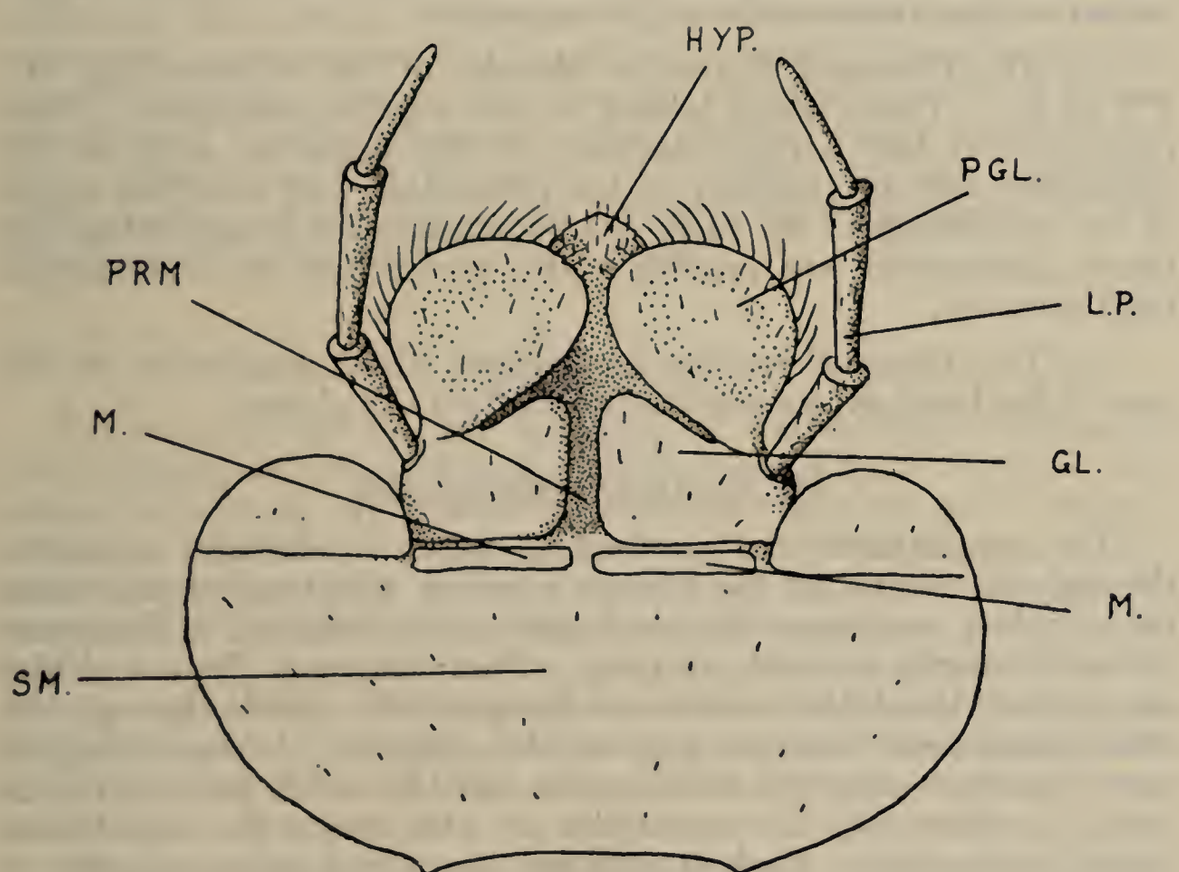

Fig. 17.—Labium of *Perla cephalotes*.

GL., glossa; HYP., hypopharynx; L.P., labial palp; M., mentum; P.GL., paraglossa; PRM., prementum; SM., submentum.

(v) *The Labium*

The labium is a broad appendage and forms most of the ventral surface of the head. It is attached by arthrodial membrane to the posterior part of the head capsule. The submentum is extended laterally in the form of flanges covering the articulating bases of the cardo and stipes (fig. 17: S.M.). Anteriorly it is attached by a membranous strip to the mentum, which is composed of two narrow rectangular sclerites. The prementa are narrow structures almost obliterated by a pair of trapezoidal glossae (fig. 17: GL., PRM.). Antero-laterally are a pair of large globose paraglossae (fig. 17: PGL.). Between the rectangular sclerites of the menta, the surface of the labium is invaginated to form an internal keel-like structure. This structure bears at its posterior end the ventral salivary cup, into which the two ducts from the thoracic salivary glands open separately. The keel also serves as the point of attachment for the paraglossal flexor muscles (fig. 14: P.F.M.) and the two pairs of hypopharyngeal compressor muscles (fig. 15: H. COM.).

Three pairs of muscles causing labial contraction are as follows:—

(a) The *Mental Retractor Muscles* (figs. 11, 14: M. R.M.) are a pair of muscles positioned slightly to one side of the midline of the labium. They originate on the sub-mental wall and are inserted on the anterior rim of the mentum.

(b) The *Proximal Retractor Muscles of the Labium* (fig. 14: PR. R.L.). These occur lateral to the mental retractors. They originate on the ventral surface of the posterior arm of the tentorium and are inserted on the premental wall near the origin of the paraglossae. As there are no muscles for labial extension, these movements are probably also performed by haemocoelic fluid pressure.

(c) The *Distal Retractor of Labium* which originates on the rear of the head capsule and is inserted on the glossae.

(f) *Mouthpart Movements*

The mouthparts during feeding follow a definite sequence throughout. Initially, the labrum is raised, while at the same time the maxillae, and especially the laciniae, are abducted as the insect moves forwards to catch its prey. Simultaneously the mandibles are opened, this latter movement being clearly visible through the semi-transparent anterior part of the clypeus. As the nymphal stone-fly nears its prey, the laciniae quickly catch and hold it in such a position that the mandibles are able to cut the prey transversely into slices. Each lacinia can be moved independently of the other. In this way, the position of the prey can be adjusted for feeding and it also ensures that the prey will not escape while it is being drawn backwards towards the mandibles. Although lacinial movement is confined to a single plane by the submentum,

within this plane two separate movements can be observed. Firstly, there is a lacinial rotatory movement, effected by the stipes adductor, whereby the stipes and lacinia as a unit rotate on a condyle situated on the posterior rim of the stipes, which fits into a groove on the anterior margin of the cardo, and secondly there is an extensory movement, whereby the maxilla as a whole is moved forward to capture and hold the prey. This extensory movement is effected by each maxilla successively, one maintaining hold of the prey, while the other is freed from the prey and extended. A knob-like condyle at the base of the cardo forms the point of articulation and rotates in a cup-like depression at the posterior end of the hypostomal suture (fig. 13: A.C. CAR.).

The movements of the labrum and of the mandibles are perfectly synchronised, the elevation of the labrum being accompanied by the opening of the mandibles and the depression of the labrum with their closure.

Hypopharyngeal movement occurs out of phase with mandibular movement. The mandibles and laciniae are ventrally concave, the concavity forming a groove normally filled by the hypopharynx. During mandibular abduction, the hypopharynx is moved upwards, its tip tending to force food particles upwards between the cutting edges of the mandibles. As the mandibles close, the hypopharynx is retracted. The setae on the ventral surface of the labrum and on the tip of the hypopharynx are so orientated as to prevent food particles moving in directions other than towards the oesophageal opening. Unlike other insects, the mandibles of *Perla cephalotes* do not possess a molar area and the food particles are not, therefore, masticated, but are swallowed whole, being pushed backwards towards the oesophagus as the hypopharynx is elevated and retracted.

(g) *Feeding*

Examination of the gut contents of the nymphal instars of *Perla cephalotes* indicates that with the exception of the first year instars, all others are almost exclusively carnivorous in feeding habits. What little vegetable matter has been found in the second and third year nymphs was found to be almost entirely composed of desmids, diatoms and some filamentous green algae. The amount of vegetable matter present was found to be so small that it might very well have been taken in during feeding on animal matter. First year nymphs however have been found with the gut full of diatoms. On no occasion has higher plant tissue been found in the gut.

The gut contents of later instars, both of those dissected, as well as those sectioned in celloidin and wax, showed that large portions of the prey are swallowed whole. Legs and sclerites of other plecopteran and ephemeropteran nymphs were abundant amongst the gut contents.

Specimens fixed in the act of feeding, and later sectioned, show that particles of insect food are not pushed into the mouth haphazardly, but are orientated so that any setae on the food particle are directed forwards, and thus do not impede its movement towards the cibarium or through the oesophagus. It is probable that the large and fleshy paraglossae play a sensory rôle in the arrangement of food particles prior to ingestion.

Feeding is effected in the following manner. The labrum is raised by the labral elevator muscles (fig. 11: LR. EL.), while the labral lobe and the roof of the oesophagus are raised by contraction of the cibarial dilator muscles and the anterior and median oesophageal dilator muscles respectively (fig. 11: CIB. DIL., A. OES. DIL.). Simultaneously, the hypopharynx is raised by the contraction of the mouth angle elevator muscles (figs. 11, 14: E.M.A.). Contraction of the hypopharyngeal depressor muscles (fig. 11: HYP. DEP.) brings the tip of the hypopharynx against the food particles, which are displaced backwards towards the oesophageal opening. Depression of the hypopharynx is accompanied by mandibular closure, the right mandible cutting in a scissor-like action inside the left. Whole food particles thus cut off, are prevented from escaping from the cibarium by the dorsally directed setae of the hypopharynx and by its lateral supralingual lobes. The hypopharynx is at this stage extended by the hydrostatic pressure of the haemocoelic fluid, while the chitinous basal rods and suspensorial rods (fig. 15: B.R., S. SCL.) give it the necessary rigidity and shape.

The passage of food through the oesophagus is accomplished by a peristaltic wave of contraction passing backwards from the cibarium to the crop. This peristaltic wave can be observed through the semi-transparent cuticle of freshly-ecdysed nymphs. As already mentioned the oesophagus is dilated by contraction of the oesophageal dilator muscles (fig. 11: M. OES. DIL., P. OES. DIL.) and constricted by the thick band of circular muscles, which are present in the wall of the oesophagus.

(h) *The Cranial Nervous System*

The cranial nervous system of *Perla cephalotes* was found to be similar in most respects to that described for the definitive type of insect by Snodgrass (1935) and to that of *Locusta* described by Albrecht (1953). A few notable differences have, however, been observed.

The brain is divided into three pairs of ganglia, comprising the protocerebra, the deutocerebra and the tritocerebra. The prognathous condition of the head is associated with the brain being rotated dorso-posteriorly and the protocerebra come to lie posterior to the deutocerebra. This condition has been described by Popham (1959) in the case of *Forficula auricularia*. On each side, each protocerebrum gives off a lateral optic nerve, which becomes enlarged to form the optic lobe before innervating the eye.

Dorsally the protocerebra give off three ocellar nerves—the two posterior ocellar nerves arising from the two protocerebral lobes (fig. 19: P. OC. N.) and the anterior median ocellar nerve from a furrow between the lobes (fig. 18: OC. N.).

In the nymph, the eyes are laterally placed and the antennae, which are directed forward, are probably the main sensory organs of the head. This is associated with the relative thickness of the pair of antennal nerves, each of which originates laterally on the deutocerebra and then runs antero-laterally to the antenna (fig. 18: ANT. N.).

The tritocerebra lie directly anterior to the deutocerebra. Antero-laterally, each tritocerebrum gives rise to a pair of labro-frontal nerves which bifurcate shortly after their origin, giving rise to the frontal connectives and the clypeo-labral nerves (figs. 18 and 19: CLP. LR. N.). The inner nerves or frontal connectives run from the tritocerebra forwards to the frontal ganglion (figs. 18 and 19: FR. G.). The outer pair of nerves run forwards and sideways to innervate the clypeo-labral muscles (fig. 19: LR. DEP., LR. EL.). On each side, the frontal ganglion gives rise to a small lateral nerve, the pharyngeal nerve, which innervates the pharyngeal wall (fig. 18: PH.N.). The antero-ventral surface of each tritocerebrum gives rise to a circum-oesophageal connective, which loops around the oesophagus and connects with the sub-oesophageal ganglion. Shortly after leaving the tritocerebra, these circum-oesophageal connectives give rise to a circum-oesophageal commissure, which forms a loop under the oesophagus and thus connects the two tritocerebral lobes (fig. 18: TR. COMM.).

The suboesophageal ganglion is as large as the brain and lies between the submentum and ventral surface of the tentorial body (fig. 18: S. OES. G.). It is connected with the brain by two thick circum-oesophageal connectives described above.

Antero-dorsally, the sub-oesophageal ganglion gives off two mandibular nerves, one on each side, while beneath each of these and slightly lateral in position, are the origins of the maxillary nerves. Each maxillary nerve bifurcates to innervate the muscles of the cardo and stipes respectively (fig. 18: MAN. N., MX. N.). From the anterior ventral surface of the sub-oesophageal ganglion two stout nerves are given off anteriorly. Each nerve bifurcates and gives rise on each side to the hypopharyngeal and labial nerves (fig. 18: HYP. N., LB. N.). Both glossae and paraglossae are innervated by distal branches of the labial nerves (fig. 18: L.B. N.).

(j) *The Stomatogastric Nervous System*

The stomatogastric nervous system is composed of a number of minor ganglia situated under the reflexed brain, the frontal ganglion lying under the anterior portion of the frons, and their

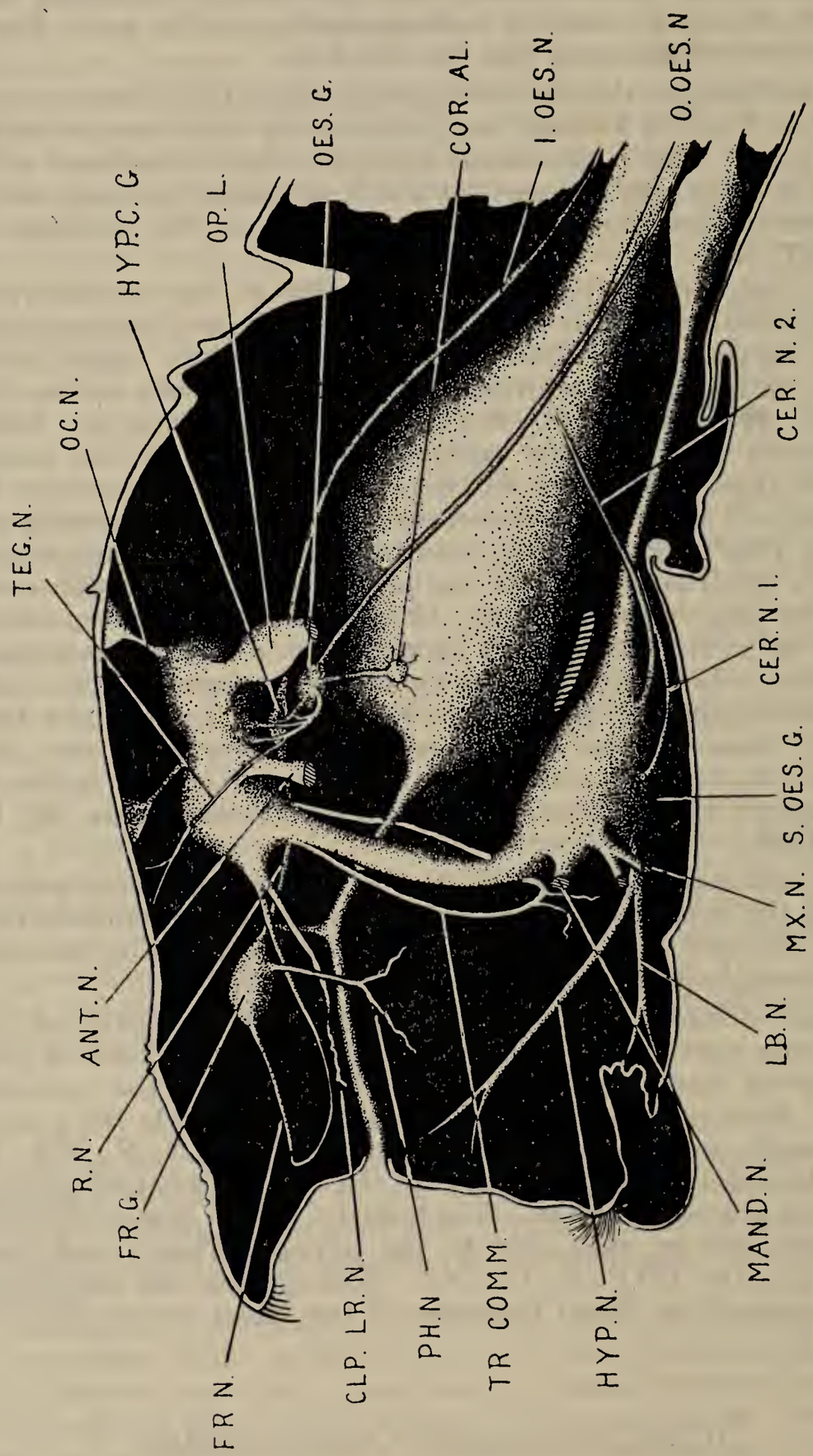

FIGURE 18 — See page opposite.

associated nerves. Though similar in many respects to the system described in *Dissosteira* by Snodgrass (1935) and *Locusta migratoria* by Albrecht (1953), quite a number of notable differences do exist.

As previously described, the tritocerebral lobes send forward frontal connectives to the frontal ganglion. Running medially backwards from the frontal ganglion is a slender nerve—the recurrent nerve—(fig. 18 and 19: R.N.), which connects with a two-lobed hypocerebral ganglion. This lies medially under the deutocerebrum and directly ventral to the aorta (fig. 18 and 20: HYPC.G.). From its posterior margin the hypocerebral ganglion sends backwards four nerves: a median nerve, which runs along the dorsal surface of the oesophagus which it innervates, a median oesophageal nerve (fig. 20: M. OES. N.), and two posterolateral nerves, which connect with the oesophageal ganglia. These two oesophageal ganglia lie, one on each side, under the protocerebral lobes. They both send backwards an outer oesophageal nerve, which runs laterally along the side of the oesophagus, through the foramen magnum and terminates in the ingluvial ganglia. These latter are attached to the gastric wall anterior to the hepatic caeca (fig. 20: O. OES. N.).

Each oesophageal ganglion sends downwards a short nerve which terminates in a corpus allatum. These corpora allata lie, one on either side of the oesophagus, directly under the brain. From the lateral surface of each oesophageal ganglion, close to the origin of the nerves supplying the corpora allata, arises a commissure, one on each side, which loops around and connects with the short anterior oesophageal nerves (fig. 20: A. OES. N.). Each of these commissures sends upwards a nerve which bifurcates to send two connectives to the ventral surfaces of the deutocerebra (fig. 20: B_1, B_2). The anterior of each of these two connectives sends dorsally, to the surface of the frons, a tegumentary nerve (fig. 18 and 20: TEG. N.) which innervates the sensory setae on the surface of the frons.

Fig. 18.—Sagittal half of the head of *Perla cephalotes* illustrating the cranial nervous system.

ANT. N., antennal nerve; CER. N. 1, cervical nerve 1; CER. N. 2, cervical nerve 2; CLP. LR. N., clypeo-labral nerve; FR. N., frontal nerve; FR. G., frontal ganglion; HYP. N., hypopharyngeal nerve; HYPC. G., hypocerebral ganglion; LB. N., labial nerve; MAND. N., mandibular nerves; MX. N., maxillary nerve; OC. N., ocellar nerve; OES. G., oesophageal ganglion; OP. L., optic lobe; PH. N., pharyngeal nerve; R.N., recurrent nerve; S. OES. G., sub-oesophageal ganglion; TEG. N., tegumentary nerve; TR. COMM., tritocerebral commissure.

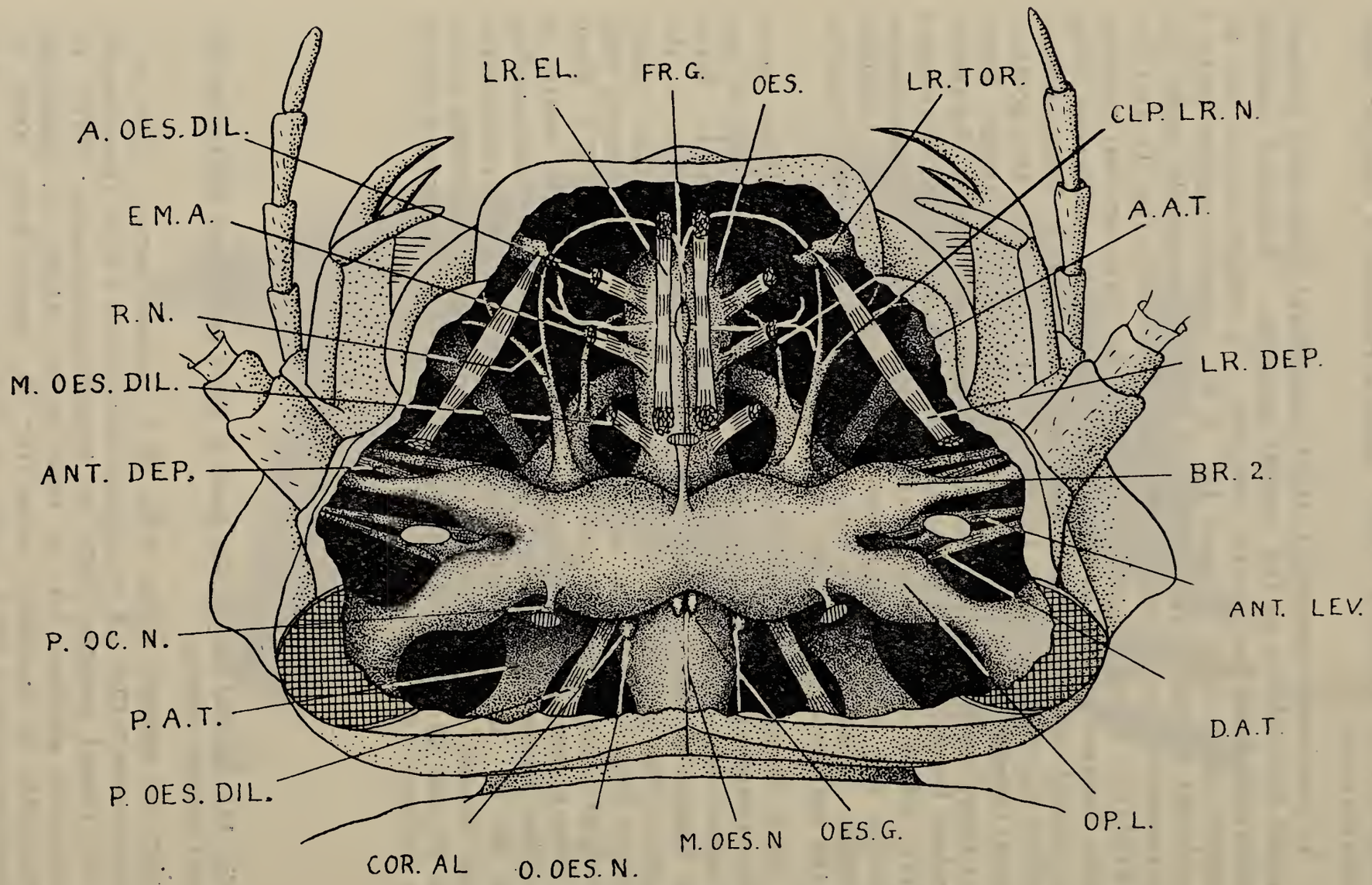

FIGURE 19. — See page opposite.

Holste (1923) found that, in *Dytiscus*, the dorsal tegumentary nerves could be traced as far back as the spongy mass of the deutocerebrum, while Hanström (1928) considers that they must arise in the tritocerebra. However, histological preparations, as well as dissection, clearly indicate that in *Perla cephalotes* the dorsal tegumentary nerves arise from the oesophageal ganglia.

The complexity of the stomatogastric sympathetic system, and the complex interconnections between the hypocerebral ganglia, the oesophageal ganglia, the corpora allata, the dorsal tegumentary nerves and the brain, call for special comment. Final ecdysis occurs after the nymphs have crawled out of the water on to dry stones bordering the stream. At this moment, a change of environment, perceived by the frontal sensory setae, may lead to a stimulation of the dorsal tegumentary nerves and thence to the sympathetic nervous system, which controls the final moult, when the nymph metamorphoses into an adult. This is an interesting possibility which merits further investigation.

(k) *The Cervical and Prothoracic Nervous System*

Posteriorly, the sub-oesophageal ganglion gives rise to two pairs of cervical nerves (fig. 21: N_1 and N_2) from its latero-ventral surface. These nerves innervate some of the muscles of the neck as well as the promotors of the cardo, which are attached to the walls of the post-genae. The prothoracic ganglion is connected with the sub-oesophageal ganglion by means of two thick connectives which run forwards over the ventral rim of the neck membrane. Laterally, the prothoracic ganglion gives rise to three main nerves on each side (fig. 21: N_1, N_2, N_3 CEP). Each anterior nerve bifurcates—one branch (fig. 21: F.E.N.) innervating the muscles of the femur, tibia etc., while the other branch arches upward to innervate the coxal muscles (fig. 21: PL. N.). Each middle nerve runs ventrally forward and sends one branch (fig. 21: CER. N_3) to innervate the proprioceptive setae of the neck membranes and also to innervate similar setae on the surface of the sternum. The posterior prothoracic nerve (fig. 21: TER. N.) runs laterally and dorsally to innervate the protergal muscles.

Fig. 19.—Roof of cranium of *Perla cephalotes* removed to illustrate the cranial nervous system.

A.A.T., anterior arm of tentorium; A. OES. DIL., anterior oesophageal dilator; ANT. DEP., antennal depressor; ANT. LEV., antennal levator; BR. 2, deutocerebrum; CLP. LR. N., clypeo-labral nerve; COR. AL., corpus allatum; D.A.T., dorsal arm of tentorium; E.M.A., elevators of mouth angle; FR.G., frontal ganglion; LR.EL., labral elevators; LR. TOR. labral tormae; LR. DEP., labral depressors; M. OES. DIL., oesphagus; O. OES. N., outer oesophageal nerve; OES. G., oesophageal ganglion; OP. L., optic lobe; P.A.T., posterior arm of tentorium; P. OC. N., posterior ocellar nerve; P. OES. DIL., posterior oesophageal dilator; R.N., recurrent nerve.

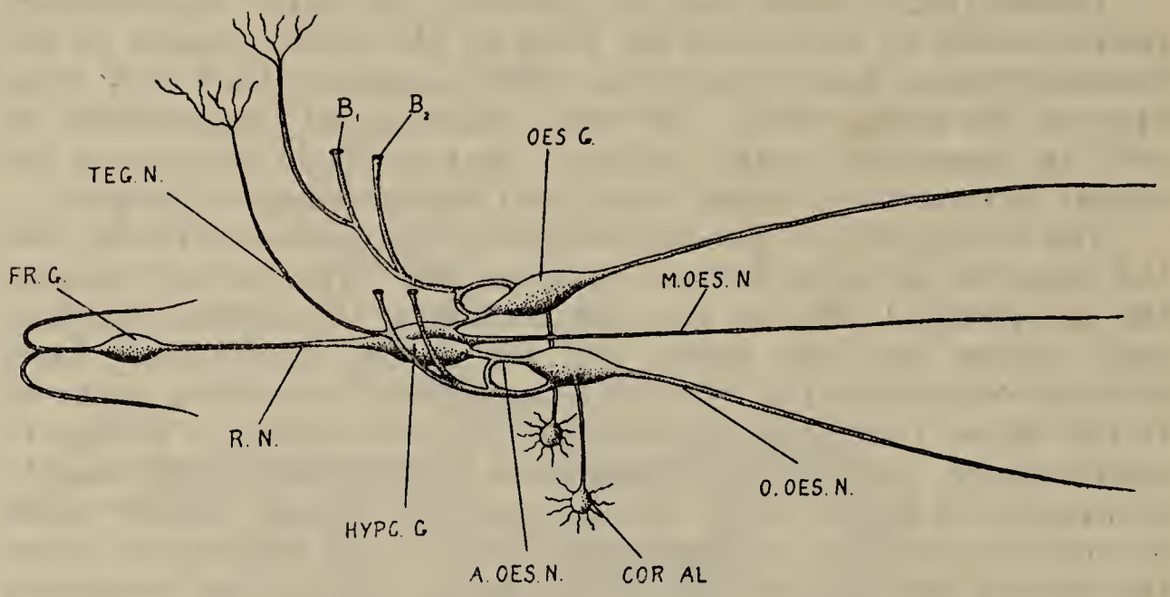

Fig. 20.—The Stomatogastric Nervous system of *Perla cephalotes.*

A. OES. N., anterior oesophageal nerve; B_1B_2, connectives to brain; COR. AL., corpus allatum; FR. G., frontal ganglion; HYPC. G., hypocerebral ganglion; M. OES. N., medial oesophageal nerve; OES. G., oesophageal ganglion; O. OES. N., outer oesophageal nerve; R.N., recurrent nerve; TEG. N., tegumentary nerve.

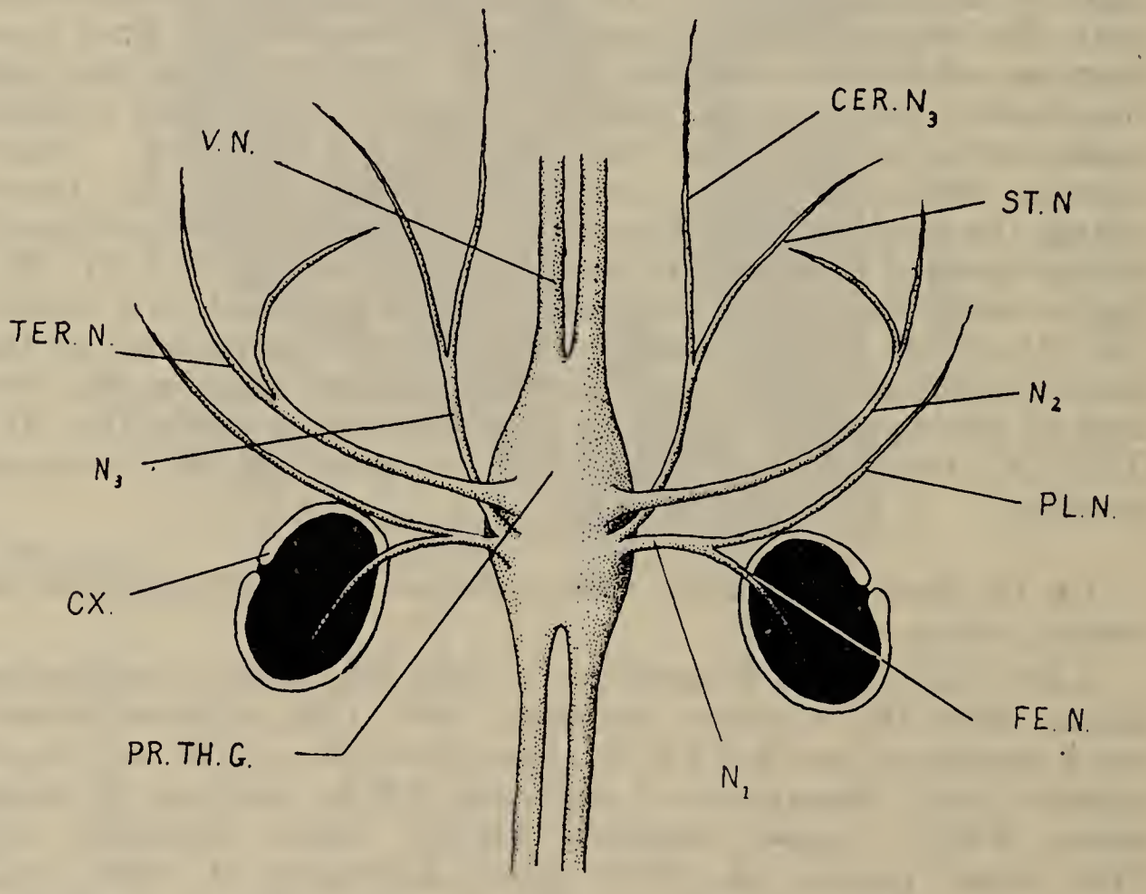

Fig. 21.—Prothoracic ganglion and its associated nerves.

CX., coxa; CER. N_1, N_2, N_3, cervical nerves; FE. N., femoral nerve; PL. N., pleural nerve; PR. TH. G., prothoracic ganglion; ST. N., sternal nerve; TER. N., tergal nerve; V.N., ventral nerve.

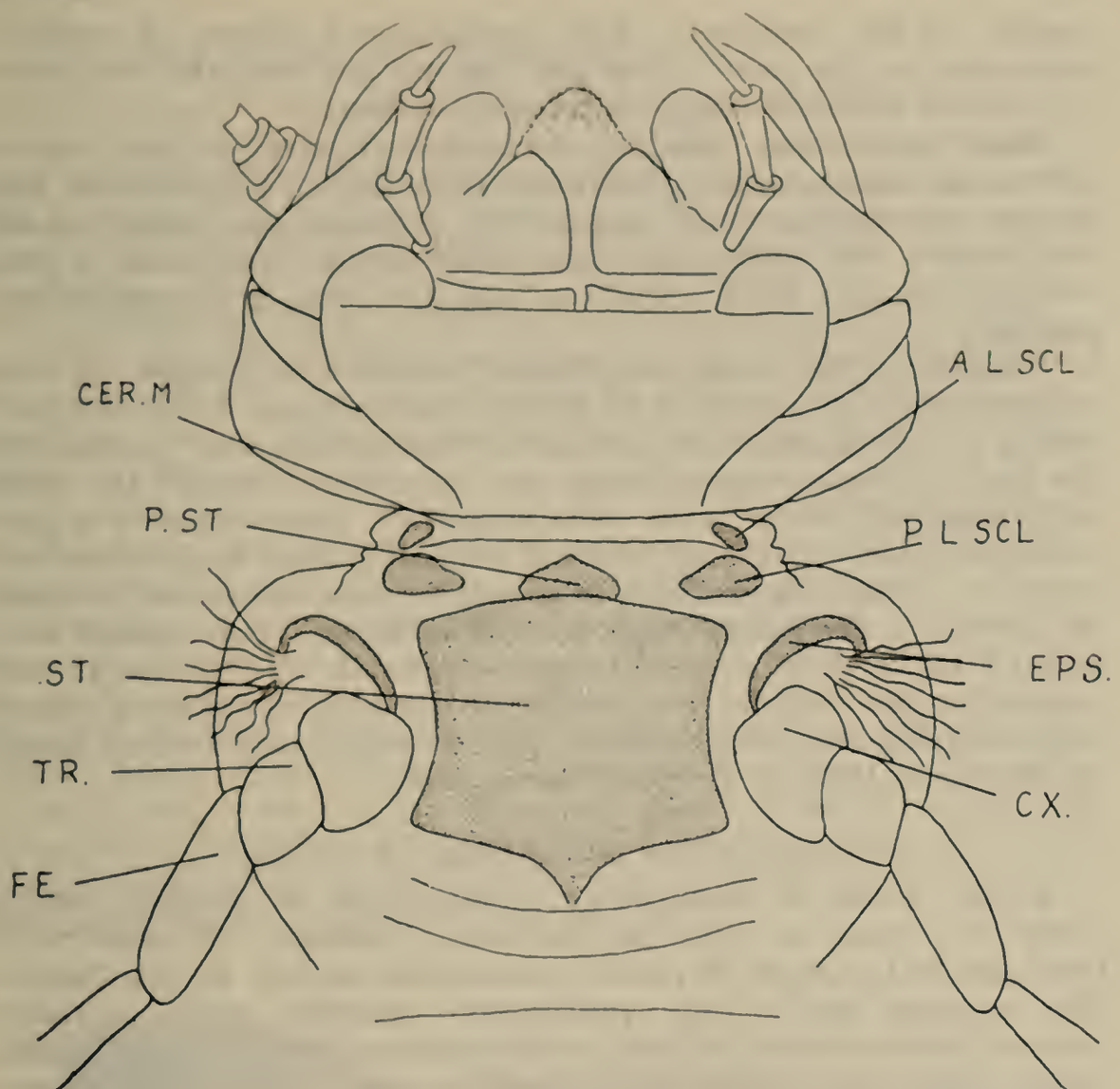

Fig. 22.—Ventral view of the neck and prothorax of *P. cephalotes* to illustrate the cervical sclerites.

A. L. SCL., anterior lateral sclerite; CER. M., cervical membrane; CX., coxa; EPS., episternum; FE., femur; PL. SCL., posterior lateral sclerite; P. ST., presternum; ST. sternum; TR. trochanter.

(l) *The Neck*

The neck of *Perla cephalotes* is covered with a narrow cylinder of much folded arthrodial membrane. This is attached anteriorly to the post-occiput of the head, both dorsally and laterally, and to the base of the submentum ventrally. Posteriorly, the neck membrane is attached to the prothoracic tergum, to a much infolded pleuron and to the ventral sternum. Except for the presence of a pair of cervical sclerites (fig. 22: A. CER. SCL., P. CER. SCL.) on either side, the neck membrane is otherwise unstrengthened. The anterior sclerites of each pair articulate anteriorly with the posterior wall of the post-occiput, while posteriorly they are hinged to the posterior cervical sclerites. These latter sclerites articulate posteriorly with the anterior lateral

margin of the sternum. This arrangement allows of vertical movement of the head while the hinging between the two pairs of sclerites facilitates slight lateral movement.

Head movement, whether vertical or lateral, is very slight, movement being mainly restricted dorsally by the anterior rim of the protergum, which completely overlaps the neck and all but touches the epicranial ridge of the head. Ventrally, a presternum (fig. 22: P.ST.) tends to keep the head in a prognathous position.

Ventrally, the neck membrane possesses a number of fine sensory setae, the function of which would appear to be the providing of information concerning the movement and position of the head. These sensory setae are connected through the neck membrane with large sense cells which are innervated by a pair of cervical nerves running forward ventrally from the prothoracic ganglion. The neck membrane is thrown into transverse folds on the dorsal, dorso-lateral and ventral surfaces. This domed surface of the arthrodial membrane is present on the dorsal and ventral surface where the membrane forms a number of superimposed folds and the condition corresponds closely to that found by Popham (1959) in *Forficula auricularia.*

(m) *Functional Morphology of the Neck*

Perla, which is exclusively carnivorous in feeding habits, holds the head in the prognathous position. Movement of the head in the vertical plane is restricted mainly by the flange-like anterior rim of the prothoracic tergum, which dorsally reaches forwards and all but touches the epicranial ridge of the head. This fact, coupled with the shortness of the neck, reduces head movements, whether lateral or vertical, within very narrow limits. Elevation and depression of the head is produced by dorsal and ventral sets of muscles running through the foramen magnum. The ventral sets of muscles producing depression of the head are as follows: —

(a) *The First Ventral Longitudinal Muscles*

This pair of muscles, running medially through the foramen magnum, originates on the apophysis of the mesosternum, being inserted on the posterior arms of the tentorium (fig. 23: No. 19).

(b) *The Second Ventral Longitudinal Muscles*

This pair of muscles, similar to, and lying directly ventral to the above, originates on the prosternal apophysis, being inserted on the posterior tentorial bridge (fig. 23: No. 13).

(c) *The Third Ventral Longitudinal Muscles*

This pair of muscles lies ventral to the second ventral longitudinal muscles. They also have their origins on the prosternal apophysis, run anteriorly and are then inserted on the ventral rim of the post-occiptal ridge (fig. 23: No. 18).

The head is raised by contraction of: —

(a) *The Dorsal Longitudinal Muscles* (fig. 23: No. 15)

A medial dorsal pair of muscles, which arise on the anterior face of the first phragma (fig. 23: PHR.), runs forward under the dorsal post-occipital ridge and is inserted medially on the dorsal wall of the epicranium and the occiput.

(b) *The Dorsal Lateral Longitudinal Muscles* (Fig. 23: No. 16)

This pair of muscles lies dorsal to the dorsal longitudinal muscles and also somewhat lateral to them. They arise on the anterior face of the phragma and are inserted on the posterior ridge of the post-occiput.

A further thin pair of muscles (fig. 23: No. 17) running dorsal to the dorsal lateral longitudinal muscles, arises on the phragma and is inserted dorso-laterally on the neck membrane.

Contraction of the *pleural neck muscles* (fig. 24: No. 1) produces lateral movement of the head. These muscles originate, one on each side, on the anterior ridge of the episternum and are inserted laterally on the post-occipital ridge. In addition, two lateral fan-shaped muscles, the *protergal muscles of the head,* cause lateral movement of the head. Each of these two muscles arises dorso-laterally on the protergal ridge and is inserted on the post-occipital ridge lateral to the points of insertion of the *dorsal lateral longitudinal muscles* (fig. 23: No. 6).

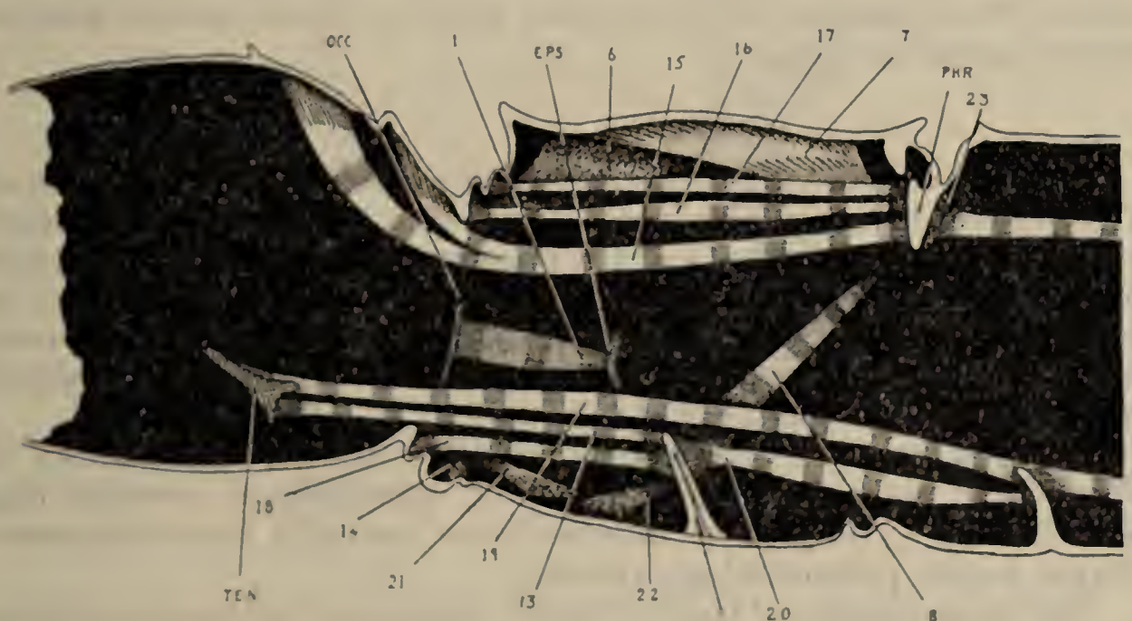

Fig. 23.—Medial longitudinal section through the head and prothorax of *P. cephalotes* to illustrate cervical and prothoracic musculature.

1, pleural neck muscles; 6, protergal muscles of head; 7, protergal muscles of the prothorax; 13, second ventral longitudinal muscles; 14, cervical membrane muscles; 15, dorsal longitudinal muscles; 16 and 17, dorso-lateral longitudinal muscles; 18, third ventral longitudinal muscles; 19, first ventral longitudinal muscles; 20, second longitudinal muscles; 21, 22, oblique ventral sternal muscles; EPS., episternum; OCC., occiput; PHR., phragma; SP., spina; TEN., tentorium.

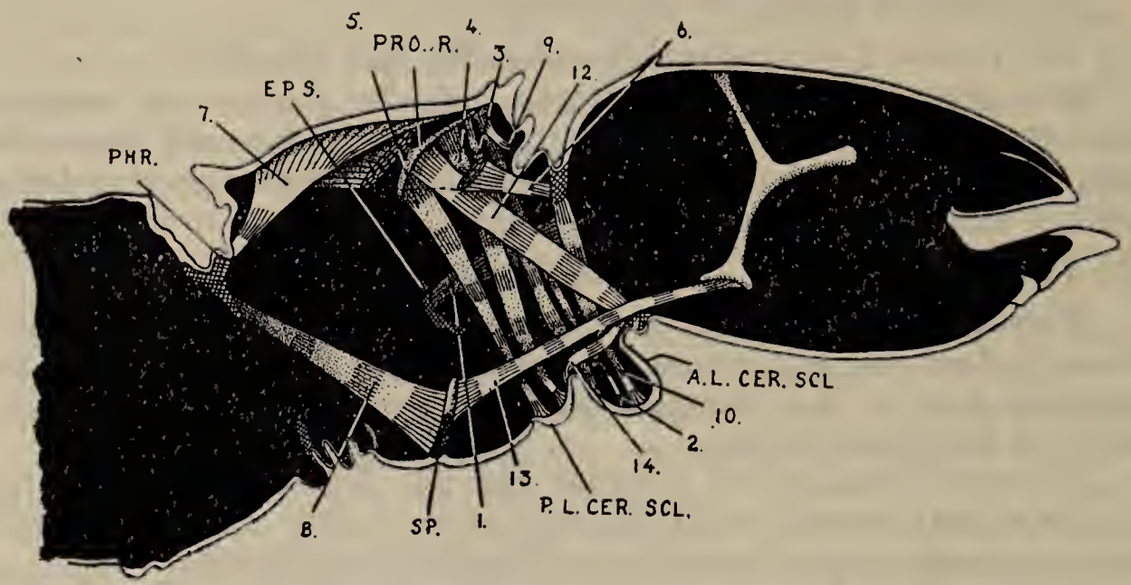

Fig. 24.—Lateral longitudinal section through prothorax of *P. cephalotes* to illustrate the musculature of the cervical sclerites.

1, pleural neck muscles; 2, 3, protergal muscles of the anterior lateral cervical sclerite; 4, 5, protergal muscles of the posterior lateral cervical sclerite; 6, protergal muscles of the head; 7, protergal muscles of the prothorax; 9, dorsal cervical membrane muscles; 10, cephalic muscles of the anterior lateral cervical sclerite; 12, protergal muscles of the head; 13, second ventral longitudinal muscle; 14, ventral cervical membrane muscles; A.L. CER. SCL., anterior lateral cervical sclerite; EPS., episternum; PHR., phragma; P.L. CER. SCL., posterior lateral cervical sclerite; PRO. R., protergal ridge.

Lateral movement of the prothorax relative to the mesothorax is produced by a similar pair of muscles, each of which arises laterally on the ventral rim of the phragma and is inserted medially on the tergal wall (fig. 23: No. 7). A similar effect is produced by two muscles, both of which arise on the phragma, one on each side. They run diagonally downwards and are inserted medially on the sternal apophysis of the prothorax (fig. 23: No. 8).

Depression of the prothorax relative to the mesothorax is effected by contraction of the second longitudinal muscles (fig. 23: No. 20). This pair of muscles runs medially from the mesosternal to the prosternal apophysis.

The musculature of the cervical sclerites and accessory muscles produces a slight rotation of the head, as well as moving the cervical sclerites relative to one another and the arthrodial membrane of the neck. The posterior cervical sclerites are drawn upwards by contraction of two slender muscles on each side of the protergal muscles of the posterior lateral cervical sclerite (fig. 24: Nos. 4, 5). These muscles arise dorso-laterally on the protergal ridge, run ventrally downwards, and are inserted on the posterior lateral cervical sclerite (fig. 24: P.L. CER. SCL.). Three slender muscles are inserted on the face of each of the anterior lateral cervical sclerites. The two posterior of these muscles, the *protergal*

muscles of the anterior lateral cervical sclerites (fig. 24: Nos. 2, 3), run dorsally and arise from the anterior rim of the protergal ridge (fig. 24: PRO. R.). The anterior muscle, the *cephalic muscle of* the *anterior lateral cervical sclerite* (fig. 24: No. 10), arises on the anterior face of the sclerite and is inserted dorso-laterally on the post-occipital ridge. Two further muscles, more medially placed, originate one on each side of the protergal ridge, run downwards and forwards, and are inserted on the latero-ventral margin of the post-occipital ridge (fig. 24: No. 12).

Ventrally two muscles aid in lateral movement of the head. These muscles arise laterally on the prosternal apophysis, run obliquely forward, cross each other and are inserted on the anterior lateral cervical sclerites (fig. 23: Nos. 21, 22).

The neck membrane as such is folded in a regular manner, during cranial elevation and depression, by two very small pairs of muscle, the *cervical membrane muscles* (fig. 24: Nos. 9, 14). The *ventral cervical membrane muscles* arise ventro-laterally on the post-occipital ridge and are inserted on the neck membrane between the anterior and posterior cervical sclerites (fig. 24: No. 14). The *dorsal cervical membrane muscles* (fig. 24: No. 9) arise dorso-laterally on the protergal wall and are inserted on the neck membrane.

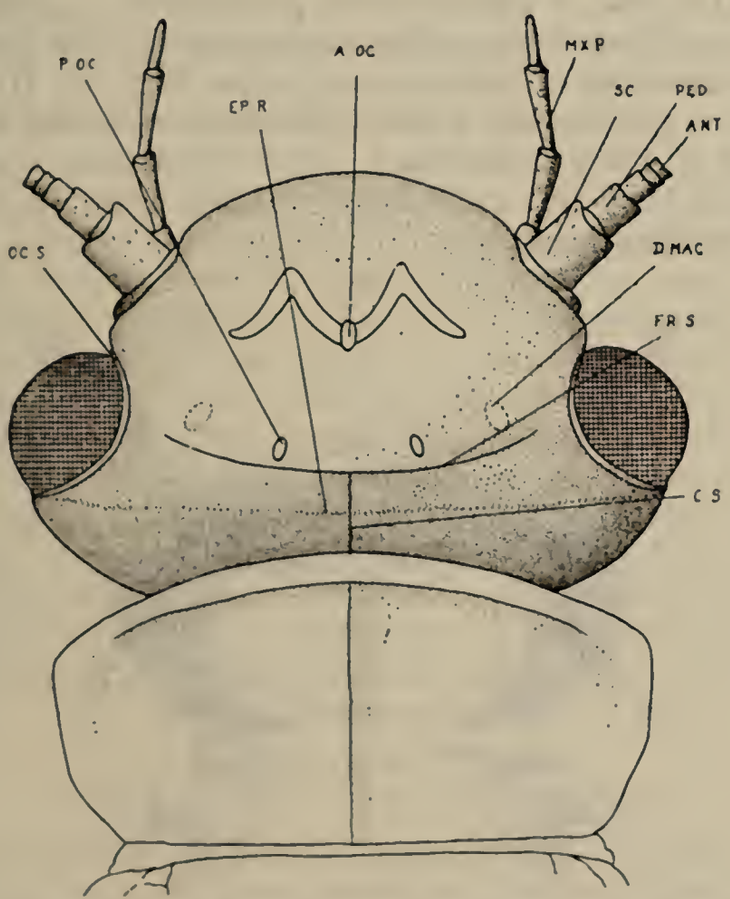

Fig. 25.—Dorsal view of the head of adult of *Perla cephalotes*.

ANT., antenna; A.OC., anterior ocellus; C.S., coronary suture; D.MAC., tentorial macula; EP. R., epicranial ridge; FR. S., frontal suture; MX. P., maxillary palp; OC. S., ocular suture; PED., pedicel; P.OC., posterior ocellus; SC., scapes.

(4) The Adults of *Perla cephalotes*

(a) *Introduction*

During the last fortnight of June, the third-year nymphs crawl out of the water on to dry stones bordering the stream and undergo their final ecdysis. The tergal, coronary and frontal sutures split open and the adult emerges. The cuticle of the freshly emerged adult is white and soft, but after a few hours the cuticle hardens and becomes greyish brown in colour.

The head of the adult is less prognathous than that of the nymph, being nearly hypognathous, and shows a striking resemblance to the head-form of the nymphs of herbivorous Plecoptera.

An examination of the adults shows that profound changes have taken place in both structure and function of the mouth parts and head capsule. Externally the head has become more globose. The dorso-ventral compression of the head and the genal expansion of the nymph are no longer in evidence (fig. 25). The bulbous paraglossae of the nymph are reduced in the adult to such an extent that they are now smaller than the glossae (fig. 26: PG. L.). The maxillae, the bases of which extend beyond the genal ridge (fig. 7: EP. R.) in the nymph, are also reduced in the adult, and lose their function as prehensile organs and acquire a form similar to that of herbivorous plecopteran nymphs (fig. 27: B.). The mandibles of the adult are peculiar. On their posterior surfaces are a number of large sensory setae (fig. 28: B). Anteriorly, they bear three small teeth which, like the rest of the adult mouthparts, are but slightly sclerotised. This weakness of sclerotisation would indicate that the mouthparts of the adult have lost their function as feeding organs.

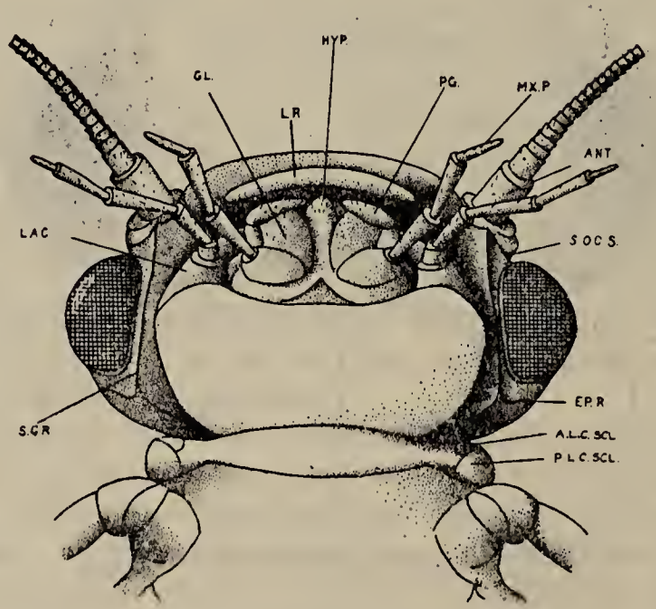

Fig. 26.—Ventral view of the head of the adult of *Perla cephalotes*.

ANT., antenna; A.L.SCL., anterior lateral sclerite; EP. R., epicranial ridge; GL., glossa; HYP, hypopharynx; LAC., lacinia; LR., labrum; MX. P., maxillary palp; PG., paraglossa; P.L.SCL., posterior lateral sclerite; S.G.R., subgenal ridge; S. OC. S., sub-ocular suture.

Fig. 27

Fig. 28

Fig. 27.—Left maxilla of adult of *Perla cephalotes*.

Fig. 28.—Left mandible of adult of *Perla cephalotes*.

This view is supported by the following facts. Firstly, no adult has been observed to feed nor were the guts of any of the specimens sectioned or dissected found to contain any animal or vegetable material. Histological preparations showed that the salivary glands are greatly reduced and the cells in an advanced state of degeneration. It seems likely that the large masses of fatty tissue, which almost completely fill the haemocoele of the adult, are produced partly from the breakdown products of mouthparts and salivary glands immediately prior to the final ecdysis. The gut showed similar degeneration, particularly in the females, where a large quantity of eggs was found to fill the abdomen.

After mating and ovipositing, the adults only survived for a few days.

(b) *The Eyes, Ocelli and Antennae*

The eyes, instead of being flattened against the sides of the head, as in the nymph, have enlarged, protrude from the side of the head, and have a number of forwardly directed ommatidia. Associated with this, the ocelli have enlarged, and protrude from the dorsal head surface. The two lateral ocelli are directed sideways, while the anterior ocellus is directed forwards. This is in contrast to the ocelli in the nymph, which are flush with the head

surface and are directed upwards. The cuticle directly above the ocelli in the adult is raised, forming a transparent cuticular lens. Due no doubt to the relatively small difference between the refractive index of the water and that of the ocellar lens, this dome-shaped lens is not needed in the nymph. Furthermore, compared with those of the nymph, the antennae of the adult are relatively reduced.

These changes would seem to indicate that in the nymph the antennae have been the main sense organs, being used to perceive prey which is then captured by the forwardly directed laciniae of the maxillae. In the adult, which appears not to feed at all, the eyes have become the main sense organs, while the antennae have partially degenerated.

(5) Discussion

Snodgrass (1935) has suggested that the hypognathous type of head may be primitive, so far as the Pterygota are concerned, because the mouthparts have a ventro-lateral position on the head capsule similar to that of ambulatory appendages. Walker (1932), after his study of *Grylloblatta,* suggested that winged insects were primitively prognathous, but Popham (1959) found that in the Dermaptera, the species having most affinity with *Grylloblatta* had a hypognathous head. Similar arguments are applicable to the Plecoptera. The nymphs of *Perla cephalotes* possess some of the most specialised mouthparts amongst the Plecoptera, while the nymphal heads differ from those of the adult in a number of significant details. Amongst the Plecoptera, the heads of the nymph and adult of *Austroperla* are very similar. Both have generalised mouthparts and a hypognathous type of head capsule; a condition which, amongst the Plecoptera, comes closest to the generalised type of pterygote head as envisaged by Snodgrass (1928 and 1935). For these reasons, the head of *Austroperla* may be taken as a primitive type from which other types of plecopteran head can be derived, no evolutionary significance necessarily being implied.

The head and mouthparts of both nymph and adult *Austroperla* are hypognathous and in this respect are similar to many herbivorous nymphs such as those of *Brachyptera* and *Capnia.* In *Austroperla* the transition from nymph to adult involves little or no change in the head. In both, it is globose and there is no indication of any flattening of the frons-epicranial region, nor of any lateral expansion of the genal region to form a flange-like lateral ridge, such as was observed in the nymphs of *Perla.* The coronary suture is long and the frontal suture, placed at the level of the hind margin of the eyes, is about one-third or more of the length of the head. The nymphal and adult mouthparts are essentially similar in structure and function. The adult mouthparts show no reduction in either size or sclerotisation. The head of *Austroperla* resembles the nymphal heads of some herbivorous Plecoptera in having a narrow labrum, while the glossae and paraglossae are both short and of equal length. Furthermore, the

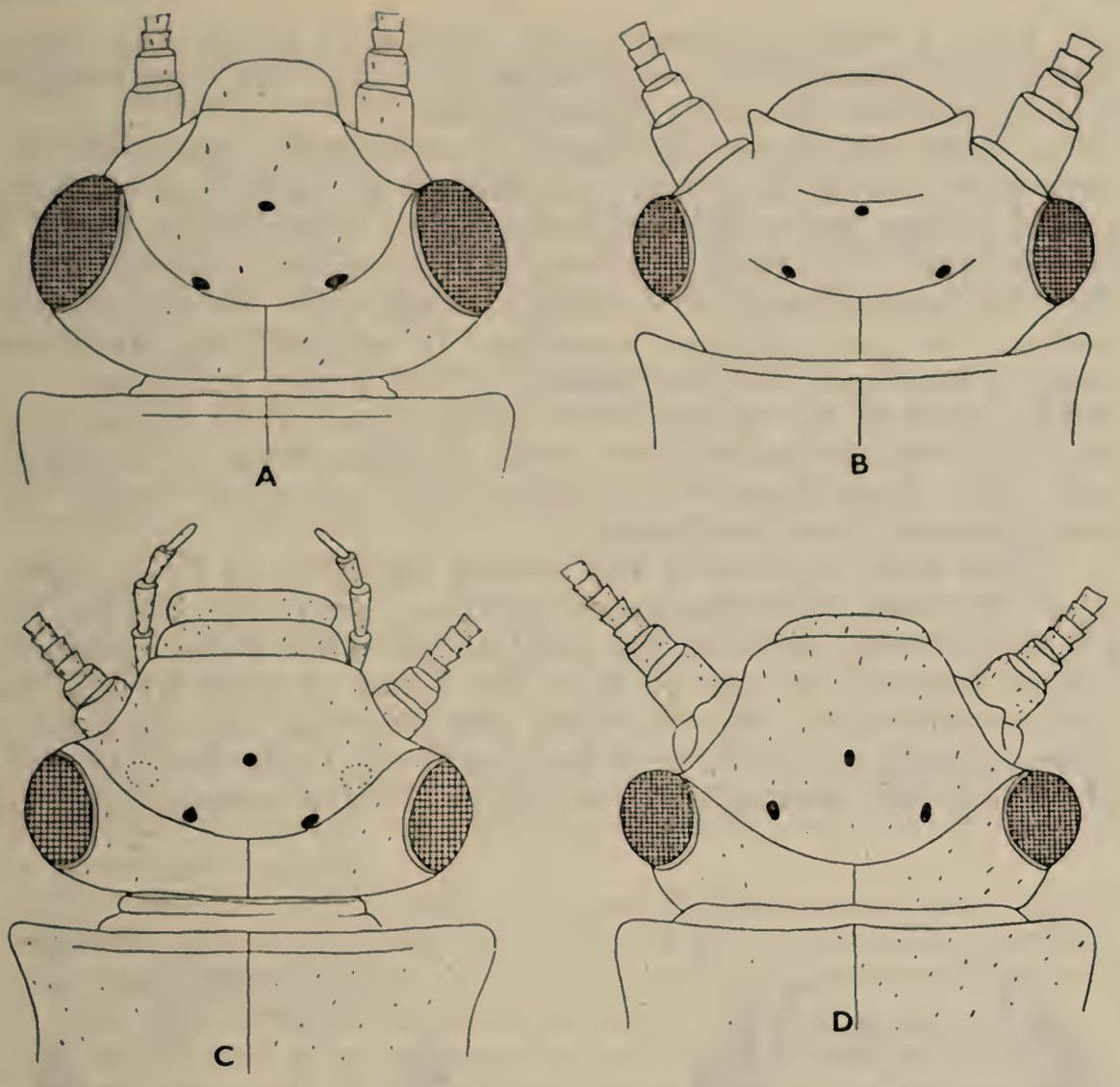

Fig 29.—A, dorsal view of the head of the nymph of *Austroperla*; C, same of *Pteronarcys*; B, dorsal view of head of adult of *Austroperla*; D, same of *Pteronarcys*.

submentum is narrow and does not extend over the bases of the maxillae (fig. 29: A, B; and fig. 30: A. B).

The head of *Pteronarcys* (fig. 29: C, D; fig. 30: C, D) may be taken as an intermediate type between *Austroperla* and *Perla*. The nymphal mouthparts of *Pteronarcys* are heavily sclerotised. The mandibles of the nymphs of *Pteronarcys* differ from those of *Austroperla* in lacking a prostheca, but resemble those of *Perla* in general structure. The mandibles of *Perla* possess two longitudinal rows of setae on the ventral surface. Between these rows there lies a shallow groove. In *Pteronarcys,* however, there is but one row of setae and no groove. The submentum is relatively broader than that of *Austroperla*. The laciniae are strong shovel-shaped structures possessing four blunt teeth at the distal ends.

The transition from nymph to adult is accompanied by some loss in the sclerotisation of the mandibles and laciniae. In dorsal view, the adult shows a striking similarity to the nymph of *Austroperla* (fig. 29: A; 29: B) while the nymph of *Pteronarcys*

(fig. 29: C) with its flattened and broadened frons, and lateral extension of the genae, would seem to occupy an intermediate position between *Austroperla* and *Perla*.

In *Perla cephalotes,* the head and mouthparts (figs. 6 and 25) show that this dorso-ventral compression of the nymph has proceeded a stage further than in *Pteronarcys*. The nymphal head is prognathous. The frons is greatly shortened and extended laterally: its lateral margins forming a flange over the articulating bases of the mandibles and maxillae. In addition, the epicranial ridge is enlarged and the flexion of the genae increased. A globose head is, by virtue of its shape, structurally strong, and the dorso-ventral compression of the nymphal head is associated with the development of internal and external ridges for strenghthening the head capsule.

It has been shown that the head of the adult of *Perla cephalotes* (fig. 6 and 25) differs markedly from that of the nymph, yet it would also appear that the head of the adult *Perla* resembles that of *Austroperla* (fig. 29 B.). The heads of both are globose and hypognathous, while the eyes and antennae take up a more anterior position that those of the nymphs of *Perla*. Furthermore, whereas in the generalised mouthparts of *Austroperla* both the

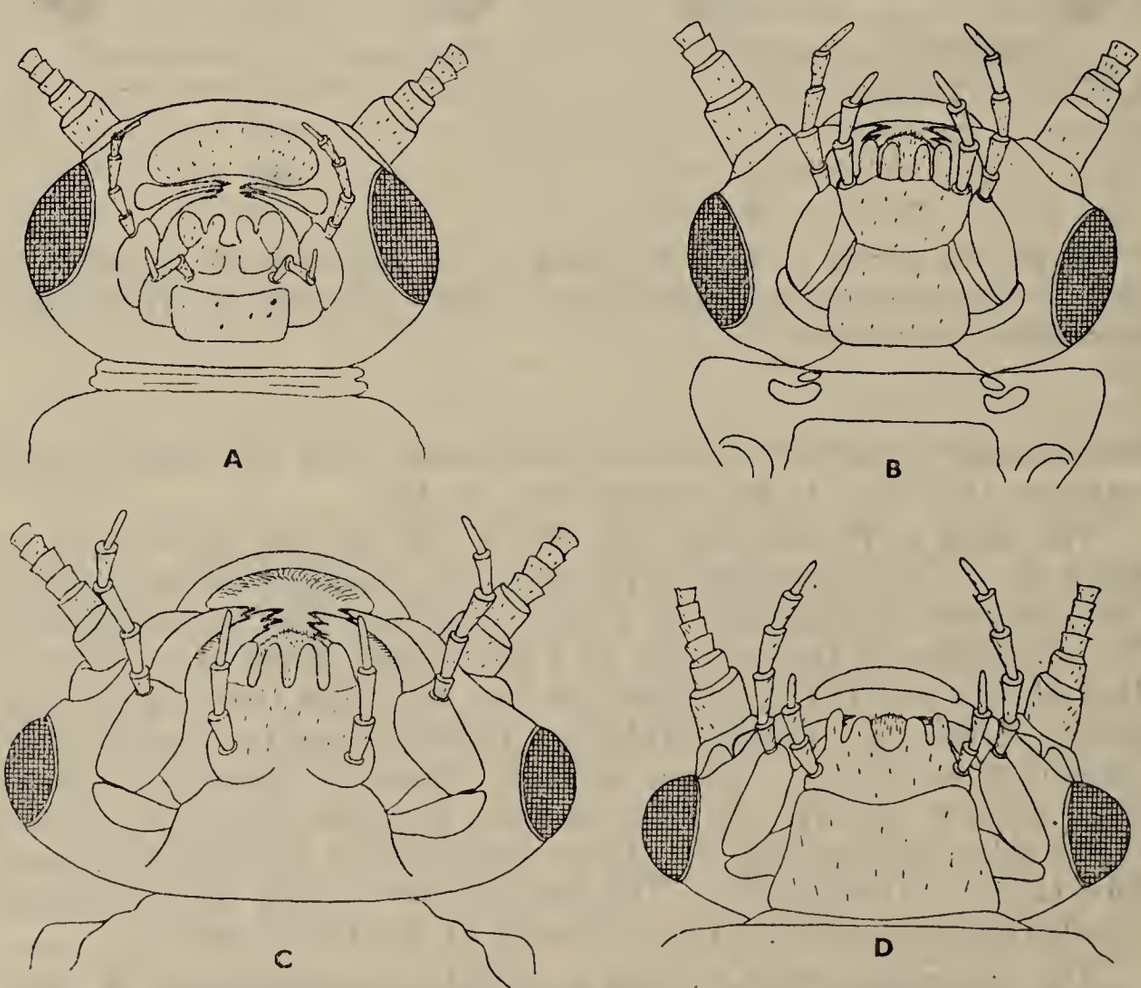

Fig. 30.—Ventral view of the head of the nymph of: A, *Austroperla*; C, same of *Pteronarcys*; B, ventral view of the head of the adult of *Austroperla;* D, same of *Pteronarcys*.

adult and nymph are very similar, in *Pteronarcys* some divergence between adult and nymph may be observed. The mandibles and maxillae of the adult are weak, unsclerotised structures, which do not seem to be used, yet the other mouthparts are similar in both nymph and adult. The submentum in both, shows a similar broadening, the glossae and paraglossae are of equal length, while both exhibit a similar expansion of the head in the genal areas (fig. 30: C, D).

In *Perla cephalotes* the divergence between the heads and mouthparts of adult and nymph has been carried a stage further. When the nymph ecdyses into the adult, the head becomes globose instead of being dorso-ventrally flattened, and these changes are associated with the disappearance of the epicranial ridge, while the lateral flange of the frons becomes rounded off and flexed ventrally. The eyes are dorsally situated in the nymph, grow faster laterally than medially and thus are directed forwards and take a more anterior position (fig. 10 and 26). This growth of the dorso-posterior region of the head capsule causes the adult head to be directed downwards and become hypognathous. In the adult, the mouthparts, and particularly the mandibles, are largely unsclerotised, become reduced and appear to lose their function

Comparison of the head of the adult *Perla cephalotes* (fig. 25) with the adult of *Austroperla* (fig. 29 B) shows that there is a great similarity between the two and that the head of the adult of *Perla* has retained a primitive form, though the reduction of the mouthparts is to be regarded as a specialisation. The fact that the heads of the adult and nymph of *Austroperla* are similar may be a primitive plecopteran feature.

Head and Mouthparts of Plecoptera

(a) *Brachyptera* and *Capnia* (fig. 3: A, B.)

Amongst the sub-order Hologhatha, Hynes (1941) states that the British species of *Brachyptera* and *Capnia* feed mainly upon algae and other vegetable material. This is in contrast with some members of the sub-order Systellognatha which are predominantly carnivorous feeders.

In *Brachyptera risi* (Morton), and *Capnia bifrons* Newman, there is a general similarity between the heads of the adults and the nymphs and in each of these species the heads also closely resemble those of the adults and nymphs of *Austroperla*. Thus the hypognathous heads have a globose form and the frontal sutures are situated about mid-way between the labrum and the rear of the head capsule. Furthermore, the mouthparts of all four species have a generalised form, though they show certain adaptations to herbivorous and algal feeding habits. In particular the mandibles bear a prostheca, have fine teeth along the median margins (fig. 32: A, B), and the inner edges of the laciniae and galeae bear many fine setae, these structures being used to brush food particles into the mouth.

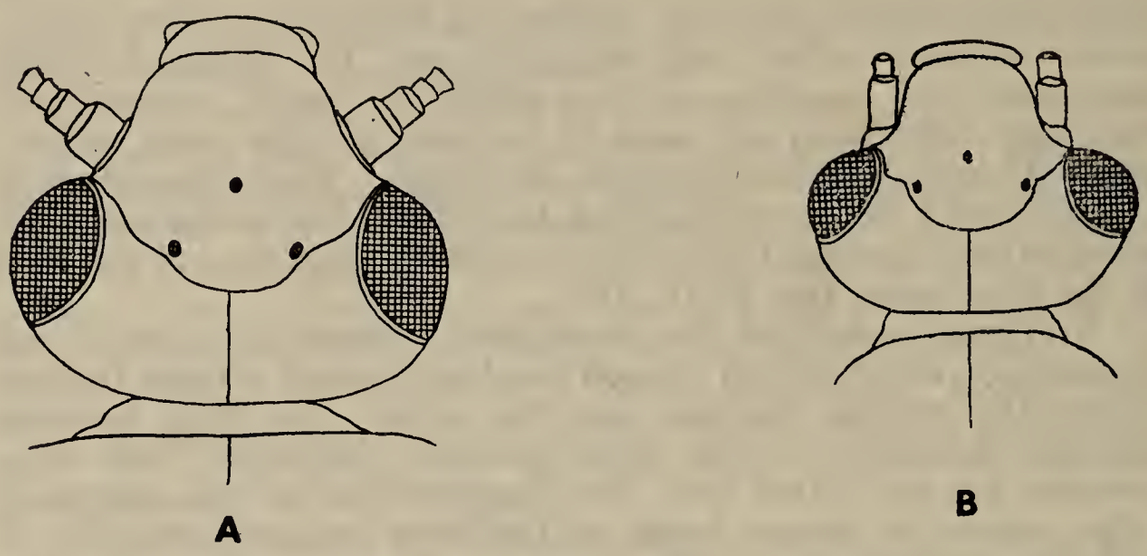

Fig. 31.—Dorsal view of the heads of the nymphs of: A, *Capnia*; B, *Brachyptera*. Similar form exists in the adults of both.

(b) *Evolutionary Trends in the Head and Mouthparts of the Plecoptera*

The most widely accepted view as to the origin of the Pterygota is that they evolved originally as a group of terrestrial arthropods, some having subsequently become adapted to the aquatic mode of life (Richard and Davies, 1957).

The primitive type of life cycle among the Exopterygota probably occurred as follows:—The eggs were laid on plants or in the soil, and both nymph and adult lived in a similar environment and had a similar mode of life. If the hypognathous type of head is to be regarded as primitive, as has been suggested by Snodgrass (1935), then it implies that the early Pterygota originally fed on plant material. In the earwig *Forficula auricularia,* Popham (1959) has shown how the mouthparts are moved during feeding, while his account of the functional morphology of the head and mouthparts of the cockroach, *Periplaneta americana,* illustrates that although mouthpart movement is practically identical the method of feeding is somewhat different.

Comparison of the mouthpart movements of the nymphs of *Perla cephalotes* with those of *Forficula auricularia* and *Periplaneta americana* indicate that they are all moved in a similar fashion, namely that maxillary movement is out of phase with the movement of the mandibles and that the rotary movement of the maxillae is in the same plane as the head.

Forficula auricularia is a specialised insect which has become secondarily adapted to feeding upon plant materials. For this reason *Periplaneta americana* may possibly be taken as exemplifying a more primitive type of Pterygote feeding habit.

That the insects originally evolved as terrestrial arthropods living in soil and litter is supported by the fact that the Myriapoda, most Apterygota, as well as many Blattids, live in this type of

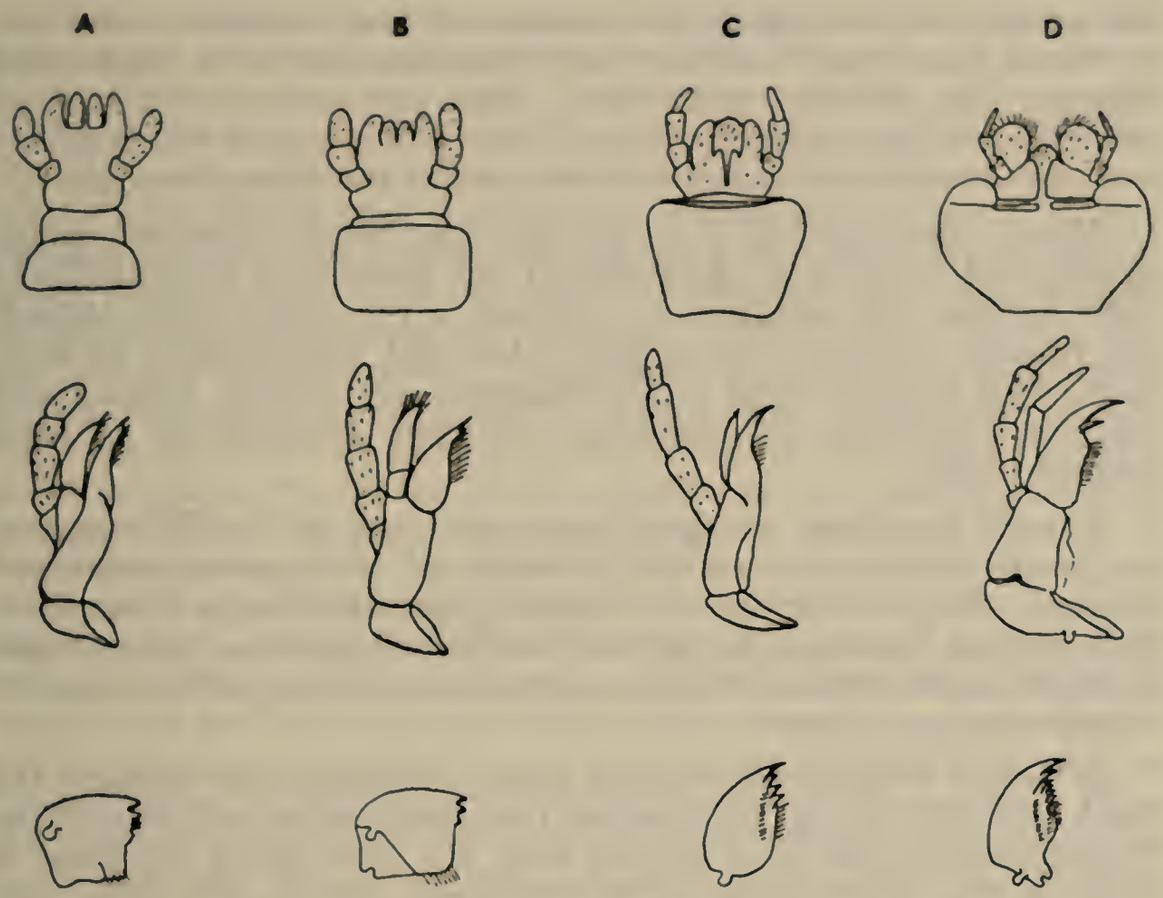

Fig. 32.—A, labium, maxilla and mandible of the nymph of *Brachyptera;* B, same of the nymph of *Capnia;* C, same of the nymph of *Chloroperla;* D, same of the nymph of *Perla cephalotes.*

habitat. The line of demarcation between soil and water is, in practice, vague and ill-defined. It has been pointed out by Popham (1960b) that the early instar nymphs of some Exopterygota were probably able to live submerged in water by respiring cutaneously. Because of their increase in size, and the greater thickness of the cuticle, later instars are only able to remain submerged for much shorter periods. It is an interesting fact that the nymphs of the Plecoptera mainly occur in rapid streams or on the shores of lakes, where the oxygen concentration is high. Unlike the nymphs of the Ephemeroptera and the Odonata, the nymphs of the Plecoptera have no special organs of respiration. Tufts of thoracic and anal gills do, however, appear in the later instars of some of the larger Perlidae, while both thoracic and jugular gills occur in smaller species, e.g. *Protonemoura,* which lives in sluggish streams, and *Amphinemoura* which lives in the silt of faster moving streams.

The primitive genus, *Austroperla,* with its generalised type of mouthparts and globose head, suggests that when the nymphs of the Perlidae firstly invaded water they fed upon detritus and other plant material. Assuming that the mouth parts were moved and used in a way similar to that of *Periplaneta,* described by Popham (*l.c.*), it is reasonable to suggest that the food material

was swept by the galeae and laciniae of the maxillae under the head and then lifted both forwards and upwards to be masticated between the closing mandibles. This movement of the food material would be accompanied by the abduction of the maxillae and the forward and upward movement of the hypopharynx.

Many members of the Hologнatha have remained plant feeders and, in the species examined, the heads and mouthparts of both nymph and adult have retained a primitive form, though the relative enlargement of the galea and proliferation of both galeal and lacinial setae of *Brachyptera risi, Capnia bifrons* and *Leuctra geniculata* Stephens are certainly adaptations to algal feeding habits.

Except for these nymphal specialisations in the Hologнatha, the heads of the adults and nymphs of the species examined have, in general, diverged but slightly from the early Plecoptera. This cannot, however, be said of the Systellognatha, the nymphs of which show trends towards carnivorous feeding which may be summarised as follows: —

Whereas *Periplaneta* collects plant material from beneath the head with the aid of the laciniae the carnivorous nymphs of the Systellognatha feed in a similar way, the prey being captured in front of the head between the forwardly directed laciniae and then pulled towards the head for mastication.

The series *Brachyptera, Capnia, Chloroperla* and *Perla,* shows a gradual increase in the relative lengths of the maxillae and particularly of the laciniae as an adaptation to carnivory (fig. 32: A, B, C. D). This elongation of the maxillae is associated with a broadening of the submentum to form a horizontal lateral groove on each side of the head. It is in these lateral grooves that the main rotary movements of the maxillae take place. These changes are associated with a reduction in the molar areas of the mandibles, while the mandibular teeth become directed towards the mid line and are used for lacerating the prey. Simultaneously, the head becomes broad and prognathous.

Dorsal views of the nymphal heads of *Austroperla, Pteronarcys* and *Perla,* show a gradual reduction of the genae with the result that whereas the frontal and occipital sutures are widely separated in *Austroperla,* they lie close together in *Perla.* This reduction in the genae has the effect of shortening the relative length of the dorsal surface of the head and thus making the head prognathous, but the reduction is also associated with the relative reduction in size of the mandibles, and the mandibular adductor and abductor muscles which originate upon these sclerites.

The enlargement of the maxillae is associated with a lengthening of the central region of the tentorium on which the maxillary adductor muscles originate. As the head becomes prognathous, there is an enlargement of the hypopharynx and its associated musculature, for lifting food particles into the mouth.

These trends in the evolution of the nymphal head and mouthparts have occurred independently of the changes in the adult. In the Plecoptera most species have a one-year life cycle, except in the Perlidae where the cycle lasts for three years. In *Perla cephalotes* the adult stage is used for reproduction and distribution of the species and it would seem that the reduction in the duration of the adult phase is associated with lack of sclerotisation in the mouthparts. The nymphs of *Perla cephalotes* are mainly carnivorous and live in rapid streams under stones. To this end the body is dorso-ventrally compressed and the antennae have become the main sensory organs. At the final ecdysis a terrestrial adult emerges. It is, however, interesting to note that the proportions and form of the head capsules of the adults of *Pteronarcys, Perla, Isoperla* and *Chloroperla* resemble those of *Austroperla,* due to a rapid growth of the dorso-posterior region of the head capsule at the time of the final ecdysis. This suggests that unlike many of the members of the Holognatha, the nymphs of the Systellognatha have become adapted to carnivorous feeding habits and the associated modifications of the nymphal mouthparts and head capsule have evolved independently of the change in form of the mouthparts and head capsule of the adults. Thus the heads of the nymph and adult of *Austroperla* closely resemble each other (fig. 29: A, B), while some degree of difference may be observed in *Pteronarcys* (fig. 29: C, D), but it is in the Perlidae that the differences between the head and mouthparts of nymphs and adults are greatest.

This study of the functional morphology of the head and mouthparts of *Perla cephalotes* and other members of the Plecoptera is of interest in showing how the adult and nymph can evolve in different ways, and that as the difference between the habitat and mode of life of the two increases, the change from immature stage to adult tends to become greater, and it is in this way that a definite metamorphosis gradually appears in the life cycle. It is for this reason that the study of the heads of the Plecoptera is not without interest, and merits further investigation.

(6) Summary

1. The nymph of *Perla cephalotes* is, except in the early instars, entirely carnivorous. To this end the head is dorso-ventrally compressed and laterally expanded, particularly in the genal area, to provide a wide base for the attachment of the muscles of the horizontally moving mandibles and maxillae. The maxillae, taking on the role of prehensile organs, are elongate, bear distally long sharp teeth and display a reduction in the size of the galeae. The mandibles are elongated medially, each bearing six sharp teeth. There is no prostheca on the inner posterior margin of the mandibles. A large fleshy hypopharynx fits into a groove formed between the concave ventral surfaces of the laciniae and mandibles. The submentum of the labium is ex-

tended laterally as a flange over the bases of the maxillae, forming a horizontal groove in which the bases of the maxillae move.

2. Maxillary movement is out of phase with that of the mandibles. Each maxilla is capable of moving independently of the other, one retaining its grip on the prey while the other draws it against the cutting edges of the mandibles. During mandibular abduction, the hypopharynx is pressed upwards and backwards. Its laterally expanded superlingulae and dorsally directed setae ensure that particles of food particles cut off by the mandibles, are pushed back towards the oesophagus. Saliva from the maxillary glands is ejected on the food through the salivary cup which is situated on the tip of the hypopharynx.

3. Haemocoelic fluid pressure plays a part in the abduction of the maxillary parts as it also does in the extension of the hypopharynx, the paraglossae and both maxillary and labial palps. Other mouthpart movements are effected by direct muscular action.

4. The cranial and stomatogastric nervous systems are similar in most respects to those of *Locusta*. The brain is, however, rotated dorso-posteriorly over the oesophagus so that the protocerebrum lies posterior to the deutocerebrum and the latter posterior to the tritocerebrum.

5. Prognathism in *Perla cephalotes* is associated with an elongation of the hypostomal region (Henson 1950). This elongation is accompanied by a corresponding elongation of the tentorium and the maxillae. These structural modifications are associated with the mandibles and maxillae becoming directed forwards.

6. The neck is short with the result that cranial elevation depression and rotation is very slight. The pro-tergum covers the neck and all but touches the epicranial ridge of the head. Cranial movement is mainly extensory and retractory, extension being effected by the hydrostatic pressure of haemocoelic fluid.

7. It would appear that primitive Plecoptera were herbivorous feeders, the head being held in the hypognathous position. The Austroperlid type would appear to resemble such an herbivorous ancestor. The transition to a carnivorous type of feeding is accompanied by the head being raised to the prognathous position; this posture facilitating prey capture by the mouthparts becoming directed forward. *Perla cephalotes* exemplifies this type. Herbivorous Plecoptera exhibit very slight metamorphosis while that of carnivorous forms is more profound, carnivorous nymphs giving rise to adults that have essentially the same structure of head and mouth parts as herbivorous Plecoptera. The nymph of *Perla cephalotes* represents the widest divergence from the primitive herbivorous type and illustrates an evolution independent of that of the adult.

(7) **Acknowledgments**

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(8) **References**

Albrecht, F. O. 1953. *The anatomy of the migratory locust.* London.

Brinck, P. 1949. *Studies on Swedish Stone-flies (Plecopt.). Opusc. ent.*

Claasen, P. W. 1931. *Plectopteran nymphs of North America.* Springfield.

Hanstrom, B. 1928. *Vergleiöchende Anatomie des Nervensystem der Wirbellosen Tiere.* Berlin.

Henson, H. 1960. On the head capsule and mouthparts of *Forficula auricularia. Proc. R. ent. Soc. Lond.*, **25**: 10-18.

Holste, G. 1923. Das Gehirn von *Dytiscus marginalis* L. *Zs. wiss. Zool. Leipzic*, **120**: 251-280.

Hynes, H. B. N. 1940. The taxonomy and ecology of the nymphs of British Plecoptera with notes on the adults and eggs. *Trans. R. ent. Soc. Lond.*, **91**: 459-557.

Imhof, E. 1881. Beiträge zur Anatomi der *Perla maxima* Scop. Aaran.

Klapalek, F. 1909. *Plecoptera* in *Brauer: Susswasserfauna, Deutschlands.* Jena.

Popham, E. J. 1959. The anatomy in relation to feeding habits of *Forficula auricularia* L. and other Dermaptera. *Proc. zool. Soc. Lond.*, **133**: 251-300.

———. 1960a. Proprioceptive setae in the neck of the common earwig (*Forficula auricularia* L.). *Proc. R. ent. Soc. Lond.*, A. **35**: 163-167.

———. 1960b. On the respiration of aquatic Hemiptera Heteroptera with special reference to the Corixidae. *Proc. zool. Soc. Lond.*, **135**: 209-242.

———. 1961. The functional morphology of the mouthparts of the cockroach *Periplaneta americana* L. *Entomologist*, **94**: 185-192.

Richards, O. W., and Davies, R. G. 1957. Imms. A.D.: *A general textbook of entomology.* London.

Schoenemund, E. 1912. Zur Biologie und Morphologie einiger *Perla* arten. *Zool. Jahrb. Anat.*, **34** (1): 1-56.

Schwermer, W. 1914. Beiträge zur Biologie und Anatomie von *Perla marginata* Scop. *Zool. Jahrb. Abt. Anat. u. Ontog.*, **37**: 267-312.

Snodgrass, R. E. 1928. Morphology and evolution of the insect head and its appendages. *Smithson. Misc. Coll.*, **80**, No. 3: 1-158.

———. 1935. *Principles of insect morphology.* New York.

Walker, E. M. 1932. Prognathism and hypognathism in insects. *Canad. Ent.*, **64**: 223-229.

Wu, C. F. 1923. Morphology, anatomy and ethology of *Nemoura. Bull. Lloyd Library*, **23**. *Entom. Ser.*, **3**: 1-81.

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